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**An investigation into the distribution of woodland invertebrates  
with particular reference to *Carabid* beetles,  
at High Beach, Epping Forest.**

By  
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A dissertation submitted in partial fulfilment  
of the requirements for the degree of  
Master of Science in Ecology.

Department of Biological Sciences.

The University of Durham.

1991

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22 SEP 1992

*This work is dedicated to the  
brother that I lost and  
to the one that I  
have found.*

## **Abstract**

Six replicate sites of *Betula* - *Fagus* were located at Epping Forest. Between June to October 1990 and April to May 1991 pitfall traps were used to sample the invertebrate fauna. Each site was surveyed and a series of environmental factors were recorded. Sorting and identification of the catch was undertaken and the invertebrate data (with particular interest in the *carabids*) was analysed using DECORANA, CANOCO and TWINSpan. The four major environmental gradients affecting *carabid* distribution were found to be : humidity, ground temperature, light and vegetation cover. Predictive equations determining species abundance under specific environmental conditions were produced and conservation implications of the work were discussed.

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## **Introduction**

### **The aims of the present work**

Epping Forest is one of the few remaining large scale tracts of ancient wood-pasture in England and the largest near-continuous block of woodland in Essex, (Webster 1991). Its importance from the point of view of nature conservation is that it may contain relict species and communities that are not found elsewhere. The Forest was traditionally managed as wood-pasture by using the technique of pollarding or 'looping' to produce a crop of wood above the reach of browsing animals, this also prolonged the life of the trees. For the last 100 years this practice has been in abeyance and there has been a large invasion of *Betula pendula* into the forest. However, it was thought that the relicts of the old management techniques might still be having an effect on the distribution of woodland invertebrates today. The present study has involved sampling for invertebrates in contrasting *Fagus* and *Betula* habitats, in order to assess the impact of traditional management techniques on the invertebrate fauna. For the invertebrates the important influence of this traditional management is its effect on the different environmental gradients. In the present study an attempt has been made to identify the important environmental gradients and relate them to invertebrate distributions and abundance. This has allowed the causal relationship between woodland management and the distribution of the woodland invertebrates to be assessed.

### **Choice of appropriate survey methods**

Whilst attempting to sample the invertebrate fauna of a locality it is as well to consider that for all practical purposes, the fauna of any given locality can be considered infinite in its diversity of species. Disney (1986), attempted to estimate the time it would take to map the entire insect fauna of the British Isles on a 10km square basis and concluded that such a task would require at least 50,000 years. Further he suggested that more realistic estimates would raise this figure by twice to ten times. It would appear that to attempt a comprehensive survey of the High Beach study sites would be folly and at best one can only hope to record a representative sample within the space of 14 months, allowed by the present study. A more constructive note from Disney *et al.* (1982), suggests that a near comprehensive survey can be made by using a range of collecting methods appropriate for different groups. Such approaches (examples of hanging dead





gulls in a woodland to attract rare *Diptera* etc.) are akin to the “maximum sampling techniques” as used by the early entomologists. The easiest method, in terms of sampling for terrestrial invertebrates is to use the pitfall trap. Disney *et al.* (1982), found that pitfall traps were selective for ground dwelling invertebrates and that although they did trap *Diptera*, greater diversities of *dipteran* species were obtained at the same site using water traps. Luff (1968) noted that the use of formalin may act as an attractant in pitfalls, selecting for some species more than others. Further, he (Luff 1986) suggested that the phenomena of aggregation in pitfall traps was probably due to both defensive secretions and sexual pheromones. Terrell - Nield (1986) identified four major factors affecting the effectiveness of pitfall traps :

- a) Population density
- b) Movement (Brownian)
- c) Pitfall boundary (absorptiveness)
- d) Outer area boundary, and the extent of its penetration by animals (probability of adsorption).

The first two of these four factors have occupied the attention of invertebrate ecologists, Baars (1979), Greenslade (1964a), and alternative approaches such as direct quadrat counts have been suggested. Den Boer (1985), undertook computer modelling exercises and was satisfied that pitfall catches from two successive reproductive seasons, produced reliable estimates of the yearly changes in the size of the local breeding populations. The present study has relied upon this evidence put forward by Den Boer.

### **The current status of Epping Forest**

Epping Forest is an area of some 2430ha, Baker *et al.* (1978) and straddles the border between Greater London and the county of Essex (National Grid Reference TL475035 to TQ405865. On the 5th March 1990, 1728ha of this site was notified as a site of special scientific interest (S.S.S.I.), under section 28 of the Wildlife and Countryside Act of 1981. The majority of the forest is owned and managed by the Corporation of London under the Epping Forest Act of the 8th August 1878, Dagley pers. com. (1991a). The study site of the present work (at High Beach) is but 12 miles from St. Paul's Cathedral.

## History of the forest

The first evidence of human habitation in the forest comes from two ancient camps, one of which the Loughton camp is within walking distance from the study sites of the present work, at High Beach. This has been dated close to 500 years B.C., Leutschner (1974). Pollen analysis and radio carbon dating of a shallow valley bog in the forest, close to the High Beach study site, have shown continuity of woodland cover over the past 4,000 years. During the Neolithic until the early Saxon times, Lime (*Tilia chordata*), dominated the woodland. Interpretations of the shift to the *Fagus - Betula* and *Quercus - Carpinus* of the present day suggest selective forest clearance during the middle of the Saxon period, when the lime decline occurred, Baker *et al.* (1978).

The earliest reference to the legal forest of Essex dates from the 1130's. Epping forest, contrary to popular belief was declared a forest not in the first phase of afforestation under William 1 but in the second phase under Henry 1. Originally the forest of Essex embraced the whole county, the boundaries being reduced or enlarged on many occasions. The chief interest for the crown lay in the deer and to a smaller extent the timber. The word forest is a legal term and describes an area of open and wooded land, Rackham (1980). The High Beach area also has open grassland areas (plains), (see the study sites location map).

Considerable wealth was generated by the crown for the crown through the establishment of deer parks. Grazing in the forest was mainly the right of individual landlords, whilst the commoner had varying degrees of access for the practice of pannage (fattening pigs on the autumn acorns) and for "looping" wood. During the Middle Ages there were constant recriminations between landlords and commoners. Courts acted as a pivot between these two factions and through which moderation of the use of the forest was maintained. Many commoners abused their rights, whilst most land lords illegally enclosed more and more of the forest land, Rackham (1978). Finally this state of affairs came to an end when the Corporation of London took up the cause of the commoners on behalf of one Tom Willingale, who had "struck blows for his ancient rights to loop wood and graze his animals", Addison (1947).

As Addison (1947), puts it "in July 1874 the Master of the Rolls affirmed the case of the Corporation of London, granting an injunction against the lords of the manors, prohibiting them from enclosing in the future and requiring them to remove all fences erected within twenty years before the commencement of the

suit. When the forest passed to the people in 1878, and was vested in the Corporation of London, the Act did not compensate the commoners for the loss of their looping rights”.

In 1833 a select committee on Public works stressed the necessity for open space in the neighbourhood of large towns for the working classes and so the Epping forest Act of 1878 gave the public open access to the forest for the first time, Layton (1985). The Act also required the conservators to “as far as possible .... protect the natural aspect of the forest”. Unfortunately, at that time the pollarded *Fagus* were regarded with strong prejudice and so the conservators neither cut them or allowed commoners to do so. The plains have overgrown and the increase in canopy shade has reduced the ground vegetation. Contrary to the requirements of the 1878 Act the forest under the management of the Corporation of London has changed more in the last 100 years than the proceeding 700 years, Rackham (1978). In Edward Buxton’s “Epping Forest” (1885), there is a species list of the flora and fauna of that time. This illustrates the decrease in wildlife diversity, with the cessation of traditional management practices since that time (as can be seen below).

### **Entomological interest of Epping Forest**

Various entomologist have shown interest in Epping Forest. Doubleday (1836), reports the presence of two butterfly species, the Marsh Fritillary, (*Eurodryas aurinia*) and the Grayling, (*Hipparchia semele*). He also comments on the Odonata and Coleoptera found in the High Beach area. Jennings (1899) notes the presence of two carabid species, *Notiophilus biguttatus* and *N. rufipes* at High Beach. Buck (1949) notes *Cychrus caraboides*, *Abax parallelepipedus*, *Bembidion nitidulum*, *Asaphidion flavipes* and others. But, it is not until 1955 that Buck produced a far more comprehensive species list for the whole forest, with notation of the exact site that individuals of different species were found. However, this remains a list with no efforts to make it quantitative. The survey methods were much more extensive than those of the study presented here, using what might be called a ‘maximum sampling technique’ whereby every possible activity was undertaken to reveal the most comprehensive list of invertebrates at that site. The work indicates that the collectors used all their practical skill to reveal the coleopterous fauna of the area. Since the methods of the present study are not comparable with those of Buck’s work, it is difficult to

determine whether his extensive species list represents an account of some species now extinct in the locality or rather that his techniques were simply better suited to discover, as near as possible the full range of coleopterous species. No doubt there is a little truth in both these possibilities. The *Eurodryas aurinia* mentioned by Jennings (1899), is now believed extinct in the High Beach locality. Furthermore, at High Beach, *Hipparchia semele* also mentioned by Jennings and the Green tiger beetle, *Cicindela campestris* mentioned by Buck (1955) are both invertebrate species generally restricted to sandy soils and are highly conspicuous, but neither was encountered over the 14 months taken to carry out the field work for the present study.

Buck (1955), records 106 species of *Carabidae* from the forest. Hammond (1979), adds a further 19 to this list. The Biological Records Centre for Essex, at the Passmore Edwards Museum adds a possible 3 new *carabid* species to this list Plant pers. com. (1991). The Nature Conservancy Council's, Invertebrate Site Register for the High Beach location adds a further 3 species, Dagley pers. com. (1991b). The present study adds three more species bringing the entire total to 134. A full list is available in Appendix 1.

Little ecological interpretation of these results was ever undertaken by the authors and it is only with the work of Hammond (1974 and 79), that such an attempt is made. He notes the effects of woodland fragmentation, with particular reference to the county of Essex and concludes that the majority of woodland of Epping Forest and parkland now occupy only some 2.5 % of the surface area of the county of Essex, and that it is "not surprising that so many woodland species are known, in Essex, from only the Epping Forest area, the only sizable tract of primary woodland", Hammond (1979).

## Methods

### Description of the study locality

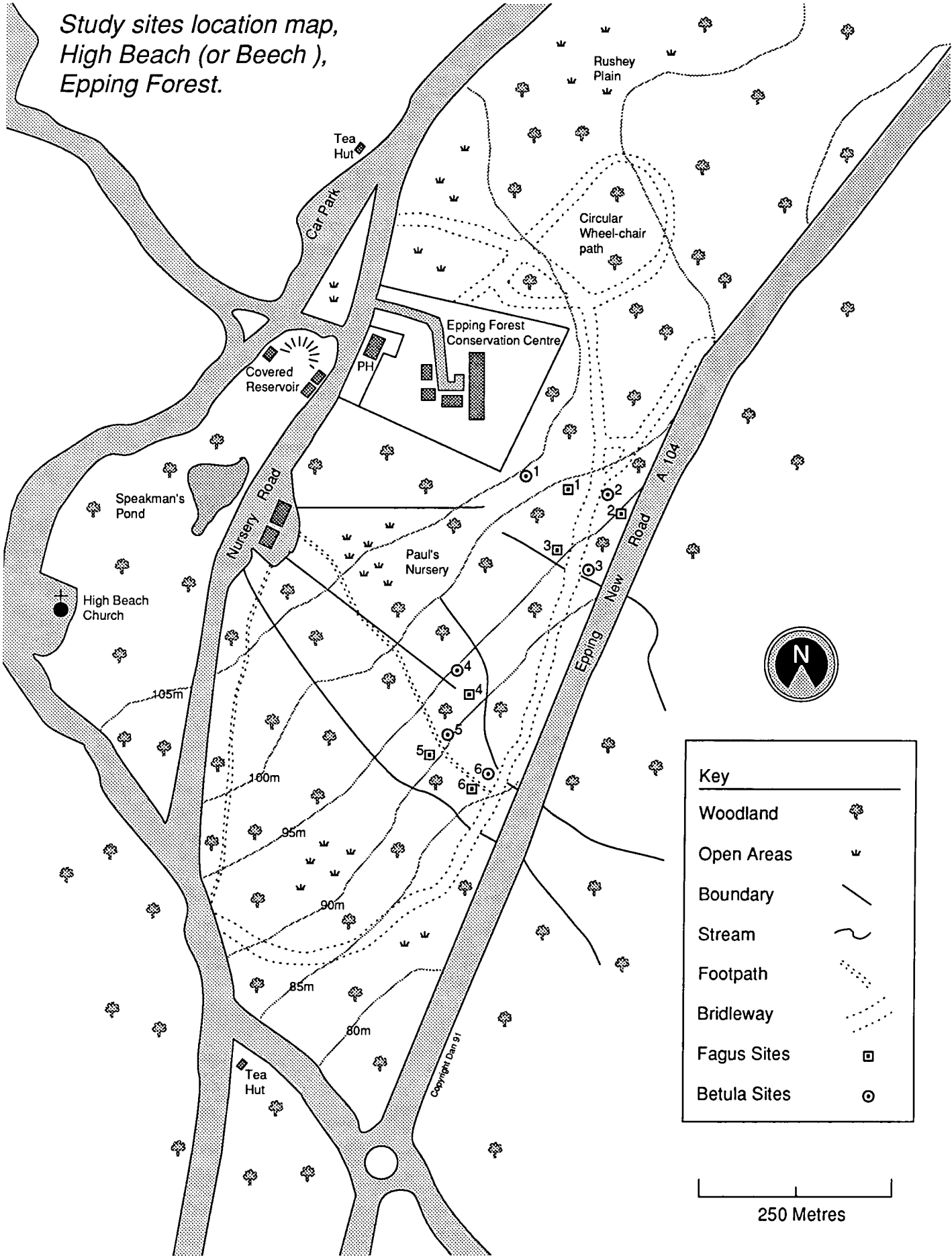
Epping Forest lies mainly on a ridge of London clay. On top of the Epping Forest ridge rest Claygate beds, consisting of inter-stratified clays and fine sands, yellow, lilac and greyish in colour. Above this are the Bagshot beds and Pebble gravel, Sturdy & Allen (1978). Topographically speaking, the land is gently rolling and on the Epping Forest ridge, a number of naturally occurring springs are present (see the study sites location map). The location of the study sites, at High Beach, is entirely underlaid by pebble gravel, Baker *et al.* (1978), on which developed paleo-argillic stagnogley soils of the Essendon series, which are considerably older than the surrounding soils, Sturdy & Allen (1978).

The majority of the forest soils are acidic, especially on the level plateau surfaces, with a thick mat of partially decomposed plant material, Brimble (1991). The forest is famous for its Beech (*Fagus sylvaticus*) pollards and the soils beneath them are usually below pH 4.0. These trees are between 200 and 400 years old and thousands are still standing despite the neglected pollarding since 1878, Rackham (1980).

Of the whole forest 1620ha is woodland, the principle tree species being : Beech (*Fagus sylvaticus*), Hornbeam (*Carpinus betulus*), Common Oak (*Quercus robur*), and Birch (*Betula pendula*), Baker *et al.* (1978). The study locality of the present work is mainly dominated by *Fagus* interspersed with *Betula* and a little *Quercus*. The name High Beach is thought to be derived from the beaches of gravel in the locality, but the spelling as in the tree is also used, Dagley pers. com. (1991b). According to classical successional theory, *Betula* is a primary coloniser, occupying the ground for less than one generation and being displaced by a "climax" tree, in this case *Fagus*, Tansley (1939). This type of succession is evident in the neglected wood pasture of Epping Forest. In recent years the hurricane winds experienced by Southern England have brought down many of the overgrown pollarded *Fagus*, their crowns having become too heavy for their shallow roots, based in loose gravel deposits. Rackham (1980), notes " in Epping Forest, where former glades and gaps created by the collapse of single ex-pollarded *Fagus* are colonised by *Betula*,..... *Betula* may become replaced by more *Betula*".

The ground cover of the High Beach area is generally sparse and under the *Fagus* little grows except some grasses, notably *Deschampsia cespitosa* and

Study sites location map,  
High Beach (or Beech ),  
Epping Forest.



*Poa annua*, and a few mosses the most obvious of these being *Leucobryum glaucum*. In the areas beneath *Betula*, a wider range of plants can be seen, but the list is still considerably restricted. It includes : *Rubus fruticosus* (agg.), *Lonicera periclymenum*, and *Pteridium aquilinum*. Along the bridle paths in disturbed soil : *Chamaenerion angustifolium* can be quite common and occasionally the rush *Juncus bufonius* and the moss *Polytrichum commune* are evident. In wetter patches *Sphagnum spp.* have been observed. Of interest historically, site 3 of the present work's study sites was unintentionally located on a drained bog, known as the "High Beach Bog", and was said to contain both *Sphagnum spp.* and *Drosera spp.*, Moxey pers. com. (1991). Equally of interest is the occurrence of Solomon's seal, *Polygonatum multiflorum* close to study site 4. It is unlikely to be a recent introduction as Buxton (1885) also records the plant close to this site. Existing as a small population, on this host is the Solomon's seal sawfly, *Phymatocera aterrima*.

Epping Forest, especially High Beach, is renowned for its rich fungal flora. The considerable quantities of dead wood and plant material littering the forest floor must contribute to this high diversity of fungal species.

### **The choice of study sites**

The sites chosen for the present study were of two types. Their distribution is shown on the 'study sites location map', while a summary of the sites environmental characteristics is given in Appendix 5. There were six sites which were composed of *Fagus* pollards. The *Fagus* trees were probably pollarded for the last time before 1878. The trees were old and the crowns mostly supported limbs which had a circumference more the size of tree trunks than the size of branches. These dense canopies drop large amounts of leaf litter, but this is mostly blown to other sites because the density of the *Fagus* within the stands was too low to trap the litter. The litter layer of the *Fagus* stands was usually sparse, with little leaf litter but some *Fagus* mast. Expressed as a percentage of the total ground cover for all the *Fagus* stands only 5.7 % was covered by vegetation. Much of this was not truly cover, 2.5 % was an unidentified *Algae spp.* growing microscopically on the bare soil. *Fagus* sites 1 and 5 had a little *Leucobryum glaucum*. While *Deschampsia flexuosa*, was found in small quantities at nearly all *Fagus* sites. *Fagus* site 3 had 13.8 % of *Juncus bufonius*, which formed the highest vegetation cover of any *Fagus* site.

Paired next to each of the *Fagus* sites was a *Betula* stand. Of these six *Betula* stands the first three were without any vegetation cover and the last three were specifically chosen because they had ground cover (mean 34.5 % of the *Betula* sites 4, 5 and 6). *Betula* stands 5 and 6 had a third of the forest floor covered by *Rubus fruticosus*. *Betula* stand 4 had 6.7 % *R. fruticosus*, but also 7.7 % *Lonicera periclymenum*, and 21.7 % *Pteridium aquilinum*. The *Betula* stands differ from the *Fagus* stands in that they are formed of very young trees/saplings, growing very close together and as a result produce shade denser than that of the *Fagus* stands. In contrast to the *Fagus* stands the *Betula* stands had a very deep leaf litter layer.

The *Fagus* pollards and *Betula* saplings form the two ends of a vegetational succession. The *Betula* forms the pioneer stage and the *Fagus* the mature stage. Descriptions in Rodwell (1991) suggest that *Betula* site 4 is a half way successional stage, with its older *Betula* and addition of *Quercus* trees, plus a ground vegetation which is by far, the most diverse of all the sites. A summary of the site characteristics can be seen in Table 1. A photographic record of the study sites was made and representative examples of *Fagus* and *Betula* sites can be seen in plates 1 to 6.

Table 1. Summary characteristics of the sites sampled at High Beach, Epping Forest.

Site number	<i>Fagus</i> stands	<i>Betula</i> stands
1	Open stand with large pollards and little leaf litter.	Small dense stand, with young trees and little leaf litter.
2	Open stand with large pollards little leaf litter.	Large dense stand, with young trees and lots of leaf litter.
3	Open and bright stand with large pollards and some ground cover.	Large dense stand, with young trees and lots of leaf litter.
4	Open and bright stand with large pollards and more leaf litter than other <i>Fagus</i> stands.	Open <i>Betula</i> and <i>Quercus</i> stand with <i>Rubus</i> , <i>Lonicera</i> and <i>Pteridium</i> , with lots of leaf litter.
5	Open stand with large pollards little leaf litter.	Large dense stand, with young trees and some <i>Rubus</i> , with lots of leaf litter.
6	Open stand with large pollards little leaf litter.	Large dense stand, with young trees and some <i>Rubus</i> , with lots of leaf litter.





Plate 1. *Betula* site 1, A small stand of *Betula pendula* with little leaf litter, note the horse riders their impact is to continually disturb the forest substrate.



Plate 2. *Fagus* site 4, The loss of a large pollard in the winter of 1990, drastically increased the light intensity at ground level. The natural gradient of the site also aids the accumulation of leaf litter, at the bottom of the incline.





Plate 3. *Betula* site 5, A larger stand of *Betula*, note the *Rubus fruticosus* which helps to retain the a deep leaf litter characteristic of a stand with a very high density of trees.



Plate 6. *Betula* site 4, These are the oldest *Betula* trees of any site, along with the *Quercus* they make this site different in vegetational terms but not in terms of the *carabid* distribution. The *Pteridium* hides *Rubus* and *Lonicera*, both of which retain leaf litter, making it dark and damp.





Plate 5. *Fagus* site 1, A large stand of *Fagus sylvaticus* with a very low density of trees.



Plate 6. *Fagus* site 6, The same site note the lack of leaf litter, any debris on the ground will be broken twigs and *Fagus* mast.

## **Environmental Variables**

### **Soil analysis**

At each site three soil profiles were taken, with the use of an auger and a descriptive record was made of the variation in colour, texture and composition of the soil at 10cm intervals. This information has been summarised in Appendix 2. The soil humus depth was recorded as recommended in the NVC field guide, with the use of a bamboo cane, which was inserted into the ground, after the leaf litter was removed. The cane was difficult to push through any more of the soil than the top humus layer and so, at the point when the cane would not go down any further, a mark would be made at the soil surface. The cane was then removed and the depth to which it had travelled was measured.

At each of the 3 soil profiles approximately 50g of soil was removed from the 10cm level and sieved to remove unwanted stones and excessive organic debris. This was returned to the laboratory for analysis. The pH was measured by adding 10g of soil to 25ml of distilled water. This 1:1.25 suspension was allowed to equilibrate for one hour. The pH was taken using a 7020 meter made by Electric Instruments Ltd., buffered with buffers of pH 7.0, 4.0 and 9.0, Hesse (1970).

From the same sample, 5 - 10g of soil was oven dried at 105 °C until a constant weight was attained (14 hours) in order to estimate the percent loss of weight on drying (water content of the soil). Then the sample was ignited at 550 °C for 5 hours in a muffle furnace and reweighed. Thus an indication of both the organic and the mineral content of the soil was attained, Hesse (1970).

### **Leaf litter analysis**

At each site the depth of the leaf litter was measured using a metre rule, one end of which was placed on the surface of the ground and the depth of the litter was read. This was undertaken twelve times, at 1m either side of each pitfall.

At 3m intervals along the pitfall transect the entire leaf litter within a 25cm<sup>2</sup> quadrat was removed and returned to the laboratory in sealed plastic bags. The contents of these bags were weighted for comparison with the leaf litter depth.

From the same sample, 5 - 10g of leaf litter was oven dried at 105 °C until a constant weight was attained (12 hours) in order to estimate the percent loss of weight on drying (this gave both the water content of the leaf litter and the dry leaf litter weight).

Lastly from each bag a 250ml sample was removed and the composition of the

litter was determined. The number of *Fagus* and *Betula* leaves were counted along with the number of *Fagus* mast. The number of rabbits at High Beach has increased dramatically in recent times and during the winter 1990 - 91 the weather was so cold and food so sparse that the rabbits took to eating the bark at the base of the tree trunks. As this heavy grazing might have an effect on the invertebrate fauna of the study sites a measure of rabbit density was made by recording the number of rabbit droppings per 250ml of leaf litter.

### **Site age and tree density**

The relative density of the trees in each stand, was undertaken by measuring the distance from each pitfall to the nearest tree. Further, the relative age of the trees in different stands was made by recording the circumference, at 1.5 metres from the ground of the nearest tree to each pitfall.

At Epping many trees have been blown down in recent years and the Corporation of London have chain sawed the trunks making it possible to count the tree rings. An attempt to relate tree circumference, which was measured for trees on each site, to the age of trees in a stand was made by counting rings and measuring the circumference of a number of fallen trees. Unfortunately no significant correlation was found.

### **Other factors**

The light intensity at ground level was measured using a Griffin and George light meter. The light probe was pointed to the sky (clear of canopy) and calibrated to 100 %, then at each pitfall the light intensity was recorded. The meter was then recalibrated before going to the next site.

The ground temperature was recorded either side of each pitfall trap using a 76mm by 1mm mercury thermometer manufactured by Philip Harris Limited. The thermometer was allowed to equilibrate with the surrounding atmosphere for 5 minutes before the temperature was recorded.

The site gradient was determined with the use of a clinometer and the aspect was derived with the use of a compass. Both sets of readings were taken from the perspective of the first pitfall trap of the pitfall transect.

The percent vegetation cover was estimated with the use of a 25cm<sup>2</sup> quadrat (for comprehensive results see Appendix 6). The Domin and Braun - Blanquet scales were not used because the impact of vegetation cover on invertebrates is

probably more important than the presence of any one species. The altitude of sites was estimated from an 1:15,000 ordnance survey map.

### **Pitfall traps**

At each site six pitfall traps were placed in the ground at 2m intervals along a linear transect. They were in the form of light brown plastic coffee cups, with a diameter of 70mm and a depth of 90 mm. In the bottom of each trap approximately 10ml of 2 % formalin, with a few drops of detergent was added. The sampling took place from the 29 May 1990 to 21 October 1990 and 17 March 1991 to 12 May 1991. The pitfalls were retrieved on a regular fortnightly basis for the spring period and on a monthly basis for the late summer. At any one site the full compliment of 6 pitfall traps was not always retrieved, partly due to trampling by horses. Occasionally whole sets of pitfalls had been removed from sites, presumably human interference. To make site comparable, means were calculated, (Appendix 3 & 4).

### **White trays and Berlese funnels**

In order to attempt to estimate the abundance of differing invertebrate groups, two additional methods were employed.

With the use a of A4 white catering tray, two handfuls of leaf litter were removed from the forest floor and were placed on the tray. This was then searched through as quickly as possible and the *carabids* observed were recorded, new samples of leaf litter were then picked up. This operation was repeated continually, at each of the 12 sites until 30 minutes had past. Results can be seen in Appendix 5.

Further samples of the leaf litter were taken from within a 25cm<sup>2</sup> quadrat, to Epping Forest Conservation Centre, where Berlese funnels were used to extract the invertebrates in the litter.

In order to get results that could have been useful for the purpose of comparison with the pitfall results of the present study, both the white tray and Berlese funnel methods proved to be too time consuming and so the attempts were abandoned. However, of the two the white tray method was the most useful in that it gave immediate results and allowed the author an opportunity to examine the microhabitat and behaviour of the *carabids* at close hand.

## **Identification and nomenclature**

The *carabids* were identified according to Lindroth (1974, 1985 and 86) The nomenclature followed Kloet and Hincks (1977), and the nomenclature of the vascular plants follows that of Clapham *et al.* (1990), whilst that for the *Bryophytes* follows Smith (1980).

Speight *et al.* (1986) and Luff (1990b), have suggested that the genus *Asaphidion* and the species *Pterostichus nigrita* respectively can be split into a number of species. No attempt has been made in the present work to pursue these lines of identification.

## **Data Analysis**

The data were subject to classification and ordination using three FORTRAN programmes, detrended correspondence analysis DCA, Hill (1979b) Ter braak (1988), Two-way indicator species analysis TWINSpan, Hill (1979a) and canonical correspondence analysis CANOCO, Ter Braak (1988).

### **Detrended Correspondence Analysis (DCA)**

This is an ordination method which allows communities to be organised in a system of coordinates so that the most similar appear closest together. DCA was developed by Hill and Gauch (1980) to correct faults of correspondence analysis, i.e. that the ends of the first axis are often compressed relative to the axis middle and the arch effect which is considered to be "a mathematical artifact with no real structure in the data", Ter Braak (1988).

Hill and Gauch (1980) overcome the compression problem by rescaling the species scores to equalise the mean-within sample dispersion of the scores at all points upon the axis, Hill (1979a). Then the sample scores are simply derived by weighted averaging. The arch affect is eliminated by detrending. This assures that at any point along the first axis the mean value of the sample scores on the subsequent axis is zero.

The result is a two dimensional chart where clustering of points indicates similar species or sites, Gauch (1986), Causton (1988). The method of detrending used was that by Ter Braak (1987). This technique was used before the TWINSpan program, Hill (1979a) in order to determine the most relevant cut - off levels on the dendrograms.

In the present study down-weighting of the relatively rarer species of *carabids*

was incorporated so that they did not bias the analysis out of proportion to their abundance, this was not necessary for the invertebrate data. The data transformations undertaken were 10, 100, 500 and 1000.

### **Two-way indicator species analysis (TWINSpan)**

TWINSpan is a robust, polythetic divisive method of classification and is applicable for data outlining the occurrence of a set of species in a set of samples (1979a). The abundance data are first ordinated using reciprocal averaging, then those species that characterise the reciprocal averaging axis extremes are emphasised in order to polarise the sample, and the samples are divided into two clusters with the ordination axis near to its middle. A perfect indicator species is one which will occur in one group of species but not the other, there are seldom perfect indicators. The best five indicators are used for the next step and indicator scores are calculated for the sample. Indicator species are those which have the highest contribution to the divisions, whilst the preferential species is one which is at least twice as likely to occur on one side of the dichotomy than the other. Only those that occur in 20 % of the samples are listed. When there is a very uneven split negative preferentials can easily occur in more samples on the positive side of the dichotomy than the negative side.

The original ordination is then redivided using species within maximum values for indicating the poles of the ordination axis. The division process is repeated on the two sample subsets to give four clusters and so on until each cluster has no more than a chosen number of members. The problem of using the actual densities of the species found in classification is that the common species tend to overshadow the less abundant but equally constant species. The use of pseudospecies has been suggested to overcome this problem, Hill (1979a). The pseudospecies cut levels used in the present study were 10, 100, 500 and 1000. TWINSpan is designed to construct ordered two-way tables identified by differential species. In TWINSpan the samples are classified first and the species are classified second using the classification of the samples as a basis, Hill (1973 and 1979a), Gauch (1986).

### **The CANOCO program**

Canonical correspondence analysis (CCA), Ter Braak (1988), is an extension of DECORANA, Hill (1979b), it visualises the relationship between species and



environmental variables. It is an extension of weighted averaging ordination, Whittaker (1967), Hill (1973), which arranges the species along axis of environmental variables. The ordination axes are constrained to be linear combinations of environmental variables. CCA distributes the species along the axis with maximal separation, the eigenvalues produced by CCA measure this separation. The output is an ordination diagram which shows the pattern of community variation and the main features of the distributions of species along the environmental variables, hence species-environment relationships can be detected.

The environmental gradients are represented by arrows which point in the direction of maximum change of each variable across the diagram.

Environmental variables with long arrows are more strongly correlated with the ordination axis than those with short axes. The position of a site or species on the CANOCO biplot in relation to the first axis and the environmental variables is assessed by its angle between and distance between the arrows.

In the present study, as with the DCA down-weighting of the relatively rarer species of *carabids* was incorporated, this was not necessary for the invertebrate data. The data transformations undertaken were 10, 100, 500 and 1000.

## Results

### The Woodland Invertebrates

During the 14 months of field work taken to gather the field data for the present study, 15,244 invertebrates were collected. All individuals were identified to order except for the *Carabidae* and *Staphylinidae* which were identified to family. A group which came to be called "Others", comprised specimens of a number of orders such as : *Mollusca*, *Pseudoscorpionidae* and *Annelida* etc. that were represented by small numbers of individuals.

The mean per pitfall, per day, per catch abundances for the major invertebrate groups can be found in Appendix 4. The differences in abundance of the invertebrate groups caught in *Betula* and *Fagus* stands is shown in Figure 1.

The most obvious difference between the two stands was of the *Opilione* abundance, the catch in *Betula*, 3559 (mean 3.39) was 7.3 times that in *Fagus*, 488 (mean 0.60) ( $t = 5.59$ , d.f. = 5,  $p < 0.01$ ). The difference between the *Hymenoptera*, 884 (mean 0.74) for *Betula* and 216 (mean 0.28) for *Fagus* ( $t = 5.41$ , d.f. = 5,  $p < 0.01$ ). All the other groups except *Carabidae* were higher in *Betula* but none were significantly so.

### TWINSpan

A TWINSpan Hill (1979a), was carried out on the mean abundances of the invertebrate data. Figure 2 shows the site classification based on the invertebrate data.

The first TWINSpan division divided the sites into predominantly the *Betula* sites and the *Fagus* sites and the second division divided a group composed of *Fagus* site 4 and *Betula* site 1, from the *Fagus* stands. In general terms *Fagus* and *Betula* form stands which are the two ends of a vegetational succession. *Fagus* stands being characterised by a few old, widely spaced trees, with little leaf litter, thus having quite dry ground conditions. The ground surface is shaded to a relatively small degree. *Betula* stands consist of young, and tightly grouped trees, with a lot of leaf litter and thus have relatively wet ground conditions. The ground surface is more shaded than the *Fagus* stands. *Betula* 1 probably falls in to the *Fagus* group because it is lacking in leaf litter (see Appendix 5). The indicator group for the first division was the *Myriopoda*, there being more in the *Betula* than in the *Fagus*. The large numbers of *carabids* in the *Fagus* stands splits this off from the group composed of *Fagus* site 4 and *Betula* site 1. *Fagus*

**Figure 1. Histogram of the totals of each invertebrate group found in both Fagus and Betula stands.**

Results from data recorded at High Beach, Epping Forest.

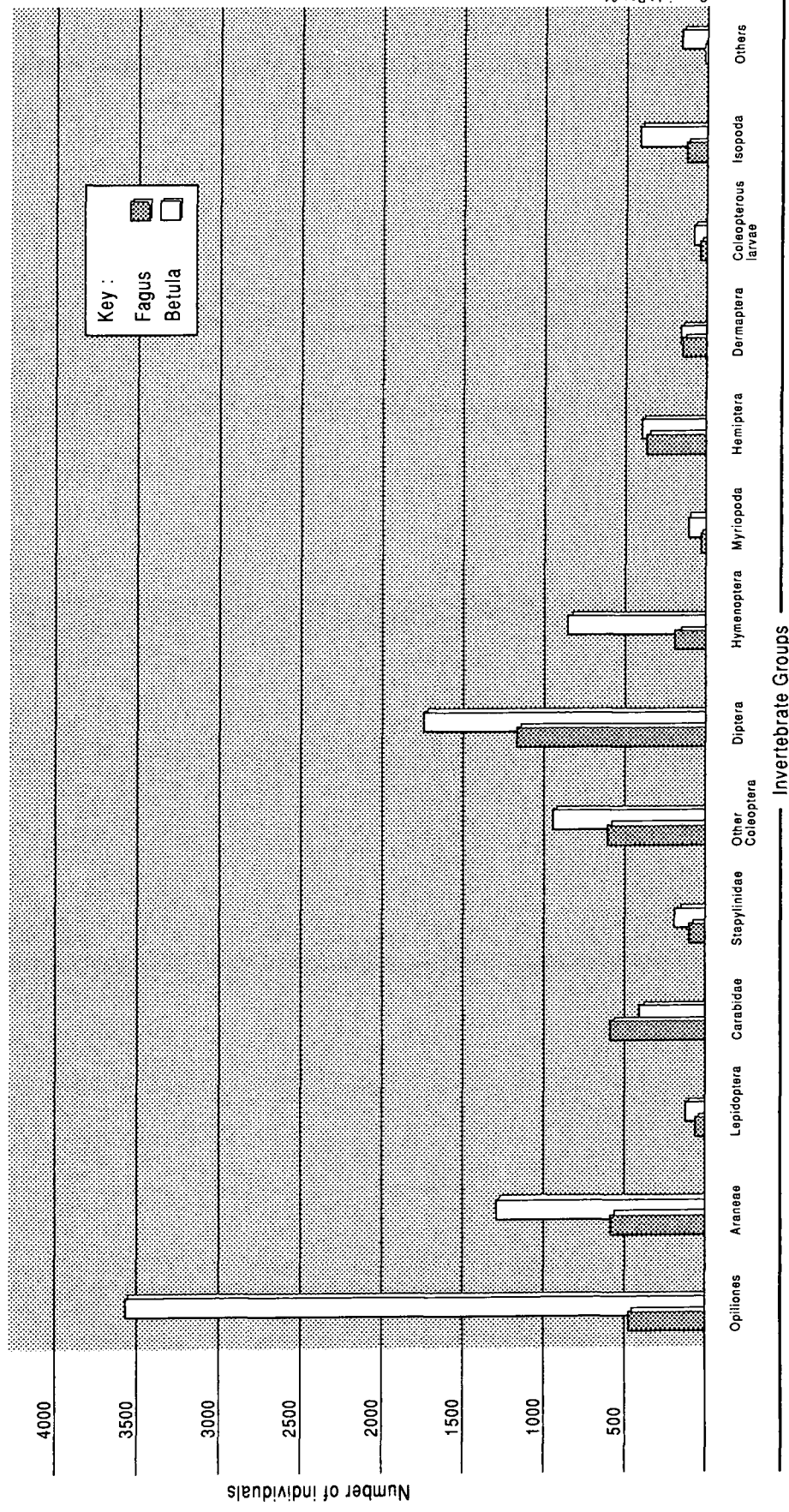


Figure 2. Twinspan classification of study sites based on Woodland Invertebrate data.

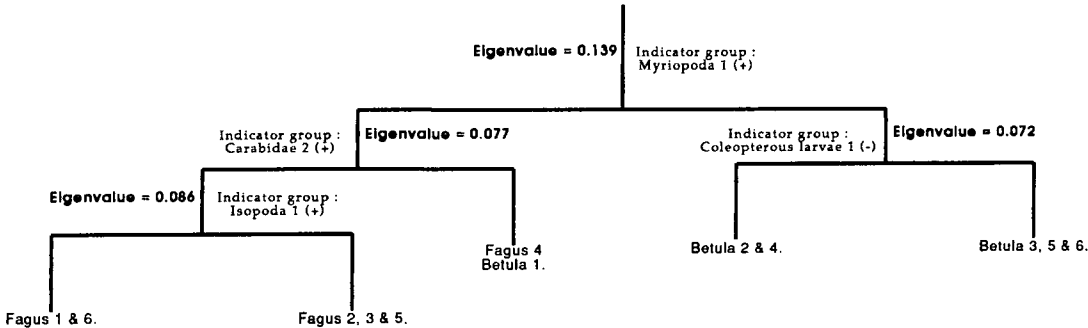
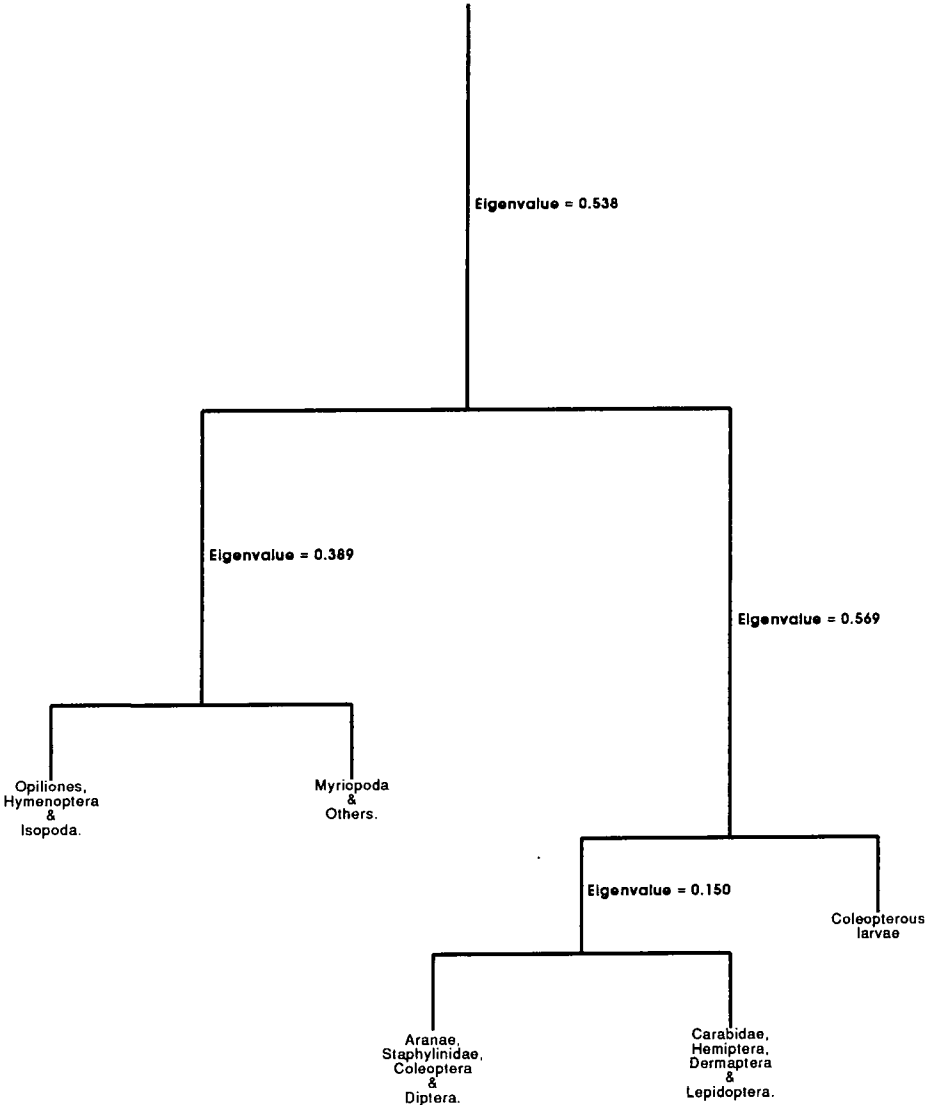


Figure 3. Twinspan classification of the major invertebrate groups in the Woodland Invertebrate data.

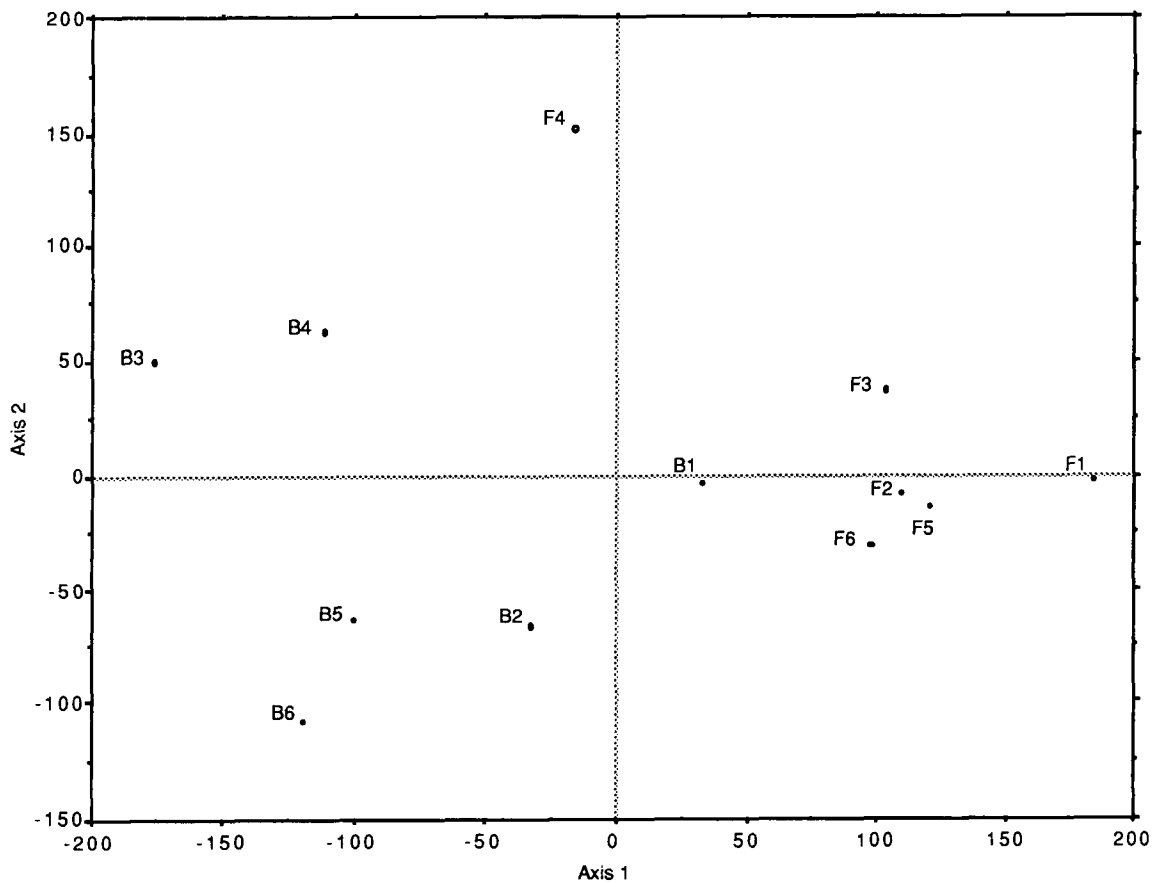


sites 1&6 and 2,3&5 are split by the rare indicator group *Isopoda*. This is true of the *Betula* sites 2&4 and 3,5&6, only in this case the indicator group is the *Coleopterous larvae*. The use of these rare indicators suggests that there is only a small difference in the invertebrate fauna as a whole between these sites. The TWINSpan classification of the invertebrate groups splits them into a spectrum from left to right. Those groups found more abundantly in the *Betula* stands are on the left and reflect the fact that higher numbers of *Opiliones* and *Hymenoptera* were caught in *Betula* (Figure 1), whilst those groups being found more abundantly in the *Fagus* stands are on the right. The middle groups, *Araneae*, *Staphylinidae*, *Coleoptera* and *Diptera*, were more generally distributed between the two, Figure 3.

### DCA

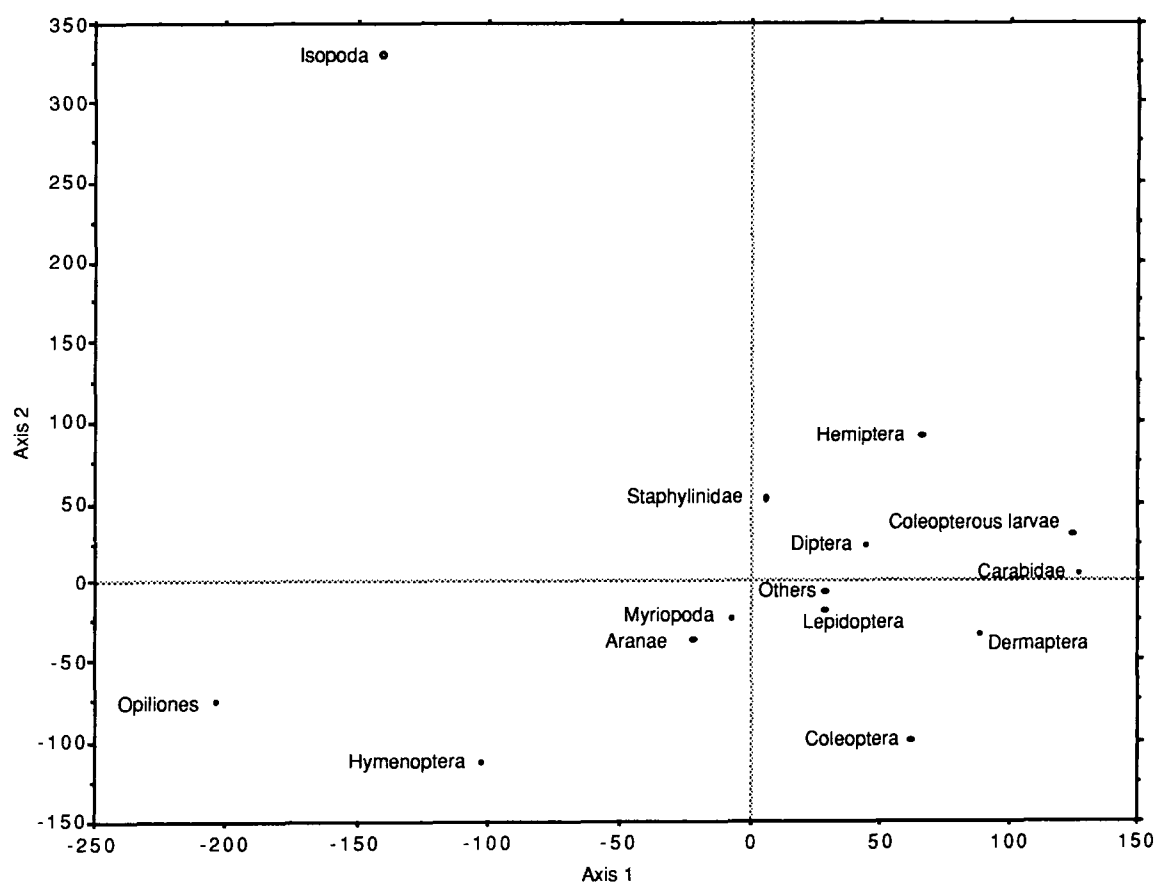
Using the Epping invertebrate data an ordination was run to show the distribution of sample sites using DCA, Ter Braak (1988) (Figure 4). Down weighting for rare species has not been used for the invertebrate data, since where this option was used, identical results were obtained. The DCA plot illustrates a spatial distribution of sites that resembles that of the TWINSpan classification. In both cases the sites are polarised into *Fagus* stands on one side and *Betula* stands on the other. *Betula* site 1 and *Fagus* site 4 are aligned in the middle of these two groups, having similar scores on axis 1. However, they are widely separated on axis two. The grouped nature of the *Fagus* sites with respect to axis 2, contrasts with the widely separated nature of the *Betula* sites with respect to axis 2.

Figure 4. DCA plot of the sample sites according to the invertebrate data, collected at High Beach, Epping Forest.



In Figure 5 the DCA plot of the invertebrates *Isopoda*, *Opiliones*, and *Hymenoptera* are to be seen to the far left (where the *Betula* sites of Figure 4 are mostly restricted) and the *Dermaptera*, *Carabidae*, and *Coleopterous larvae* are seen on the far right, where most of the *Fagus* sites are located. Other groups are in the middle. This compares well with the TWINSpan classification. The first axis probably reflects the increase from right to left in leaf litter depth.

Figure 5. DCA plot of the invertebrate groups, from data collected at High Beach, Epping Forest.



### Environmental variables

The invertebrate distribution were related to the environmental variables using CANOCO, Ter Braak (1988). Eighteen environmental variables had been measured. In order to select a small number to enter in the CANOCO analysis Pearson's correlations were carried out to determine covariables. (Table 2).

Table 2. Results of a Pearson's correlation matrix (18 x 18 variables inspected, only results where  $p \leq 0.005$  are included here, the sign indicates whether the correlation was positive or negative).

<b>DLW</b>	- 0.001								
<b>LD</b>	+ 0.001	+0.001	- 0.001						
<b>SpH</b>				- 0.004					
<b>CNT</b>		- 0.005							
<b>DNT</b>		- 0.001			+ 0.001				
<b>LLW</b>		+0.002				- 0.005			
<b>NBL</b>						- 0.005	+ 0.002		
<b>NFM</b>	- 0.003	- 0.003	+ 0.003	- 0.001		+ 0.005			
<b>SMC</b>								- 0.001	
<b>SWC</b>									- 0.001
	<b>WCOLL</b>	<b>DOSHL</b>	<b>DLW</b>	<b>LD</b>	<b>CNT</b>	<b>DNT</b>	<b>LLW</b>	<b>SOC</b>	<b>SMC</b>

**KEY :** WCOLL = water content of leaf litter, DOSHL = depth of soil humus layer, DLW = dry leaf litter weight, LD = leaf depth, SpH = soil pH, CNT = circumference of nearest tree, DNT = distance to nearest tree, LLW = leaf litter weight, NBL = number of *Betula* leaves, NFM = number of *Fagus* mast, SOC = soil organic content, SMC = soil mineral content, SWC = soil water content.

Covariables were placed into groups and one variable from each group was run in a sequence of CCA's to extract the most important variables to give the highest eigenvalues for axis 1. This technique is recommended by Ter Braak (1986).

## CCA

The results of the CCA run on the invertebrate data for axis 1 and 2 can be seen in Table 3 and 4 respectively, the plot of these results can be seen in Figure 6.

Table 3. Results of a CCA of the invertebrate groups for the 1st axis, from data collected at High Beach, Epping Forest.

<b>Environmental variable</b>	<b>Regression coefficients</b>	<b>t-values</b>	<b>Interset correlations</b>
Leaf litter water content	- 96	- 582	- 899
Light	14	73	25
Vegetation cover	- 8	- 40	- 514
Number of <i>Fagus</i> leaves	- 17	- 84	- 322



Table 4. Results of a CCA of the invertebrate groups for the 2nd axis, from data collected at High Beach, Epping Forest.

Environmental variable	Regression coefficients	t-values	Interset correlations
Leaf litter water content	23	288	3
Light	- 28	- 297	- 513
Vegetation cover	- 35	- 375	- 698
Number of <i>Fagus</i> leaves	- 11	- 116	- 131

N.B. the values in these tables have been multiplied by 100

The water content of the leaf litter was the most important variable influencing axis 1 which showed a significant relationship between invertebrate distribution and the selected environmental variables ( $p < 0.04$ , Monte Carlo permutation test). Vegetation cover is the most important factor on the second axis and lastly light intensity being the principle variant on the third axis is obscured on this two dimensional plot (of axis 1 and 2). Quite clearly the *Betula* sites are damper than the *Fagus* sites (c.f. Appendix 5) and the invertebrates reflect this in their distribution. Equally *Betula* sites 4, 5 and 6 are those which have a greater vegetation cover than the other sites, seemingly the invertebrates are affected by this as well. From this analysis the importance of ground level humidity becomes clear. The weighted correlation between leaf litter water content and axis 1 was -0.9 suggesting that the major gradient affecting the distribution of woodland invertebrates is a humidity gradient. Of secondary importance was the presence of ground vegetation.

Other none, vegetation

Figure 6. CCA plot of the sample sites according to the invertebrate data, collected at High Beach, Epping Forest (the arrows represent the strength and direction of environmental gradients).

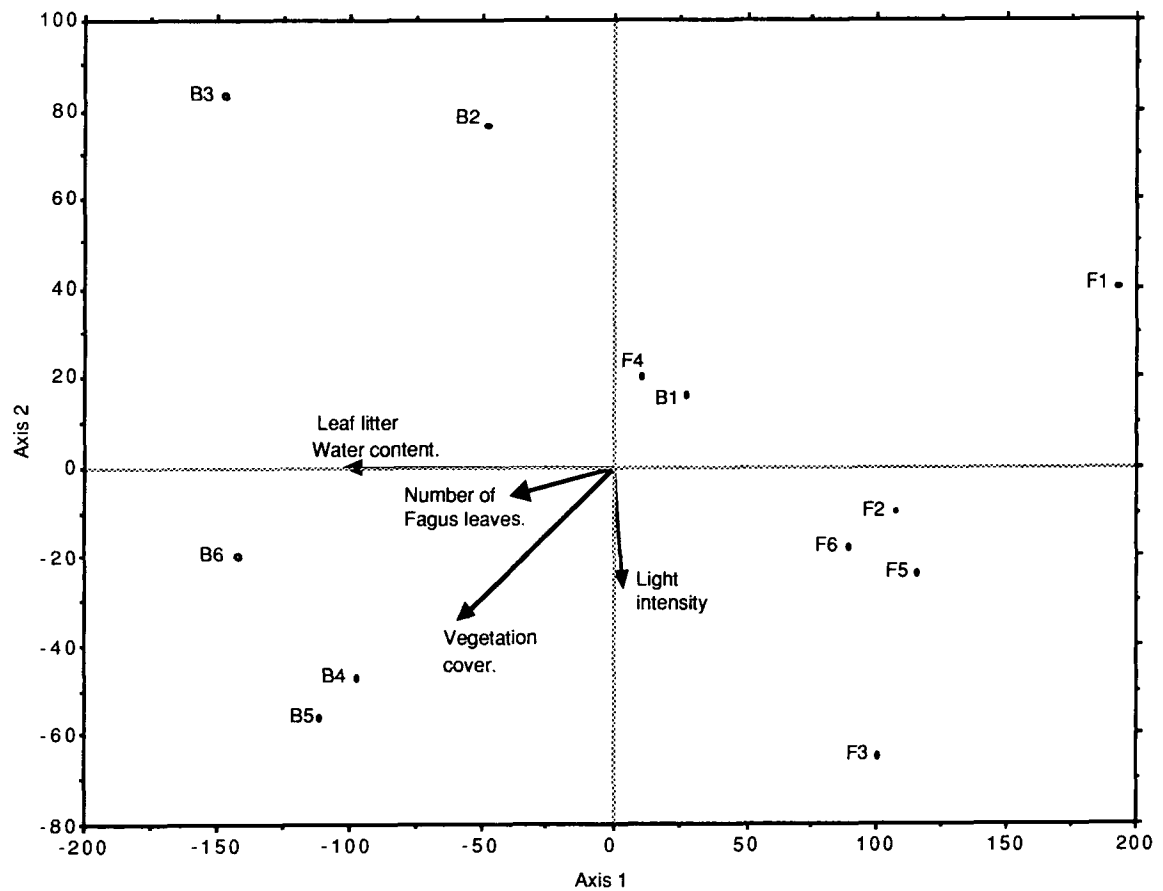
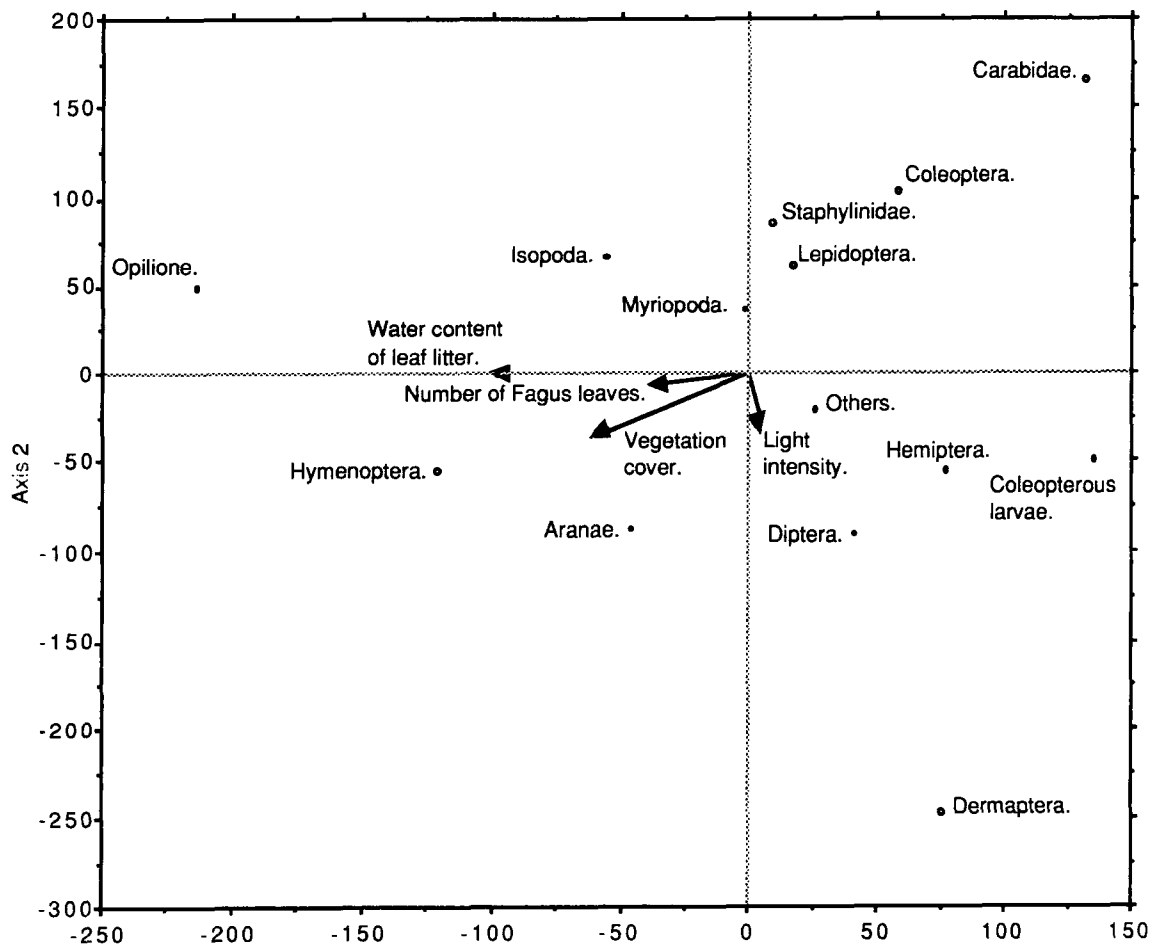


Figure 7 shows the distribution of invertebrate groupings in the CCA. Firstly in comparison with the DCA plot of Figure 6 the distribution of the invertebrate groups in relation to axis 1 is similar to that in the DCA. The correspondence is less good for axis 2, suggesting the environmental variables were having a constraining influence. However, this does not greatly affect the interpretation. In ascending order, the *Opiliones*, *Hymenoptera*, *Isopoda* and *Araneae* show a

preference for high humidity, positively correlated with leaf litter depth. Equally the abundance of the following are negatively related to the same factor, also in ascending order : *Carabidae*, *Coleopterous larvae*, *Coleoptera*, *Hemiptera* and *Dermaptera*.

Figure 7. CCA plot of the invertebrate groups, from data collected at High Beach, Epping Forest.



The other invertebrate groups were fairly neutral in their reaction to the influence of this factor. The vegetation cover has a positive influence on the *Hymenoptera*, *Opiliones* and the *Araneae* and a negative influence on the *Coleopterous larvae*, *Carabidae* and the *Coleoptera* (in ascending order). Light intensity seems to have its most positive affect on the *Dermaptera* and its most negative affect on the *Opiliones* and the *Isopoda*.

### **Woodland *Carabid* species**

The first part of this study concentrates on the analysis of the major taxonomic groups of woodland invertebrates. Species identification allows predictive work to be more specific in its application. For this task the *Carabidae* were chosen and twenty nine *carabids* were identified to species.

Although Figure 8 shows that in all more *Calathus piceus*, *Nebria brevicollis* and *Notiophilus biguttatus* were caught in the *Fagus* stands, while greater numbers of *Abax parallelepipedus* and *Carabus violaceus* were caught in the *Betula*.

There was considerable variation between sites and only *Abax parallelepipedus* numbers were significantly higher in one type of stand (*Betula*) than the other (paired  $t = 2.8$ , d.f. = 5,  $p < 0.05$ ).

### **TWINSPAN**

The first TWINSPAN division divided the sites into *Fagus* and *Betula* groups and here the indicator species were *Abax parallelepipedus* on the *Betula* side and *Calathus piceus* on the *Fagus* side reflecting their relative abundance in the two types of woodland (Figure 9). In contrast with the TWINSPAN classification produced by the invertebrate data, *Fagus* site 3 is split off from the main groupings and *Fagus* site 4 is reincorporated into the general *Fagus* grouping where *Betula* site 1 also remains.

The species classification (Figure 10) selects recognisable groupings from respective *Fagus* and *Betula* stands. This classification can be best interpreted with reference to Table 5, which illustrates the percentage of each species of the total catch at both *Fagus* and *Betula* sites and expresses the difference as a ratio. *Fagus* sites have a greater number of *carabid* species than the *Betula* sites (c.f. Figure 14 and Table 5). This is despite the greater abundance of invertebrates at the *Betula* sites, for which the total mean for the whole sampling period was : *Betula* 10.5, *Fagus* 6.1.

Figure 8. Histogram of the totals of each Carabid species found in both Fagus and Betula stands.

Results from data recorded at High Beach, Epping Forest.

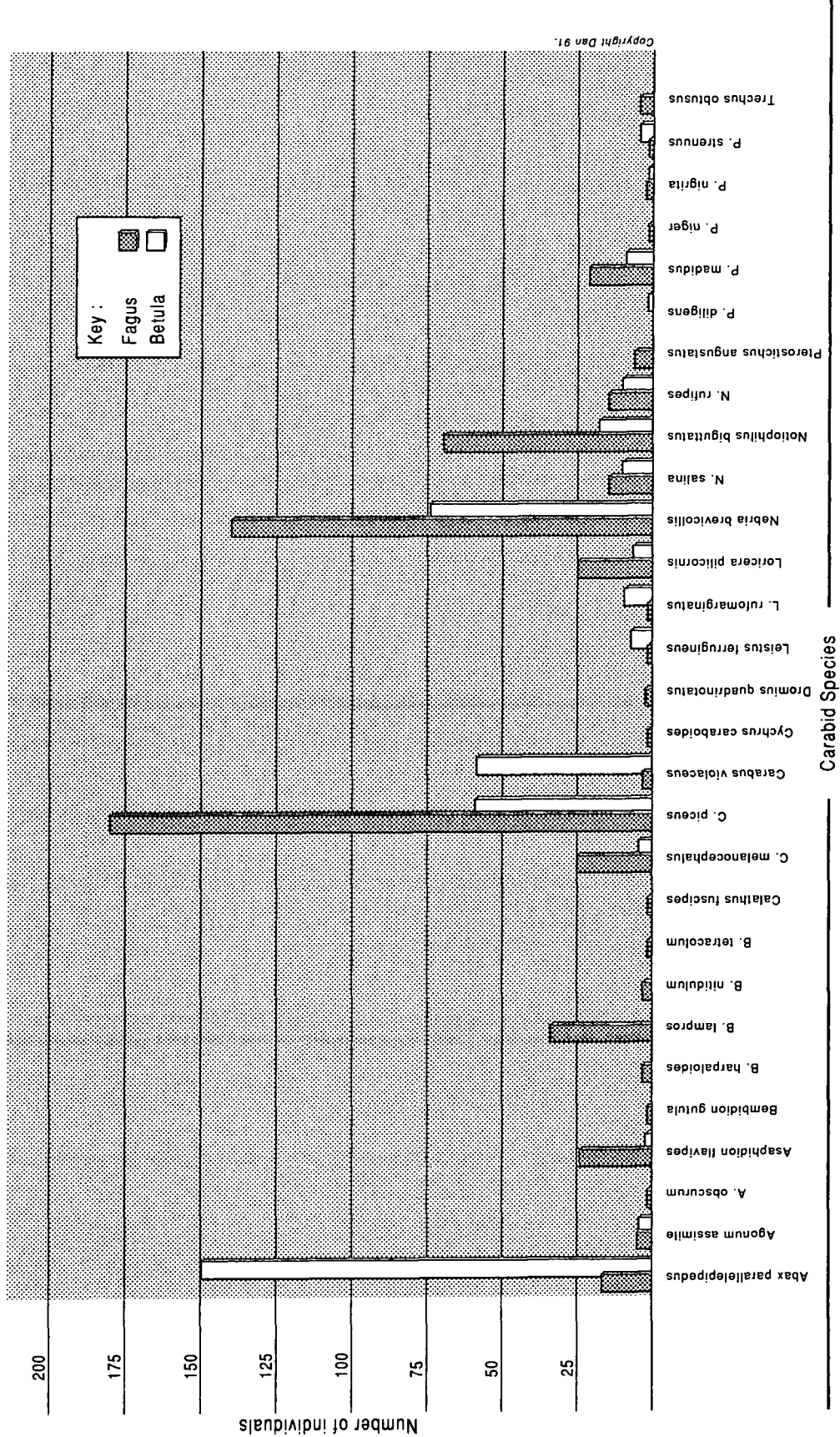


Figure 9. Twinspan classification of sites according to carabid data, sampled at High Beach, Epping forest.

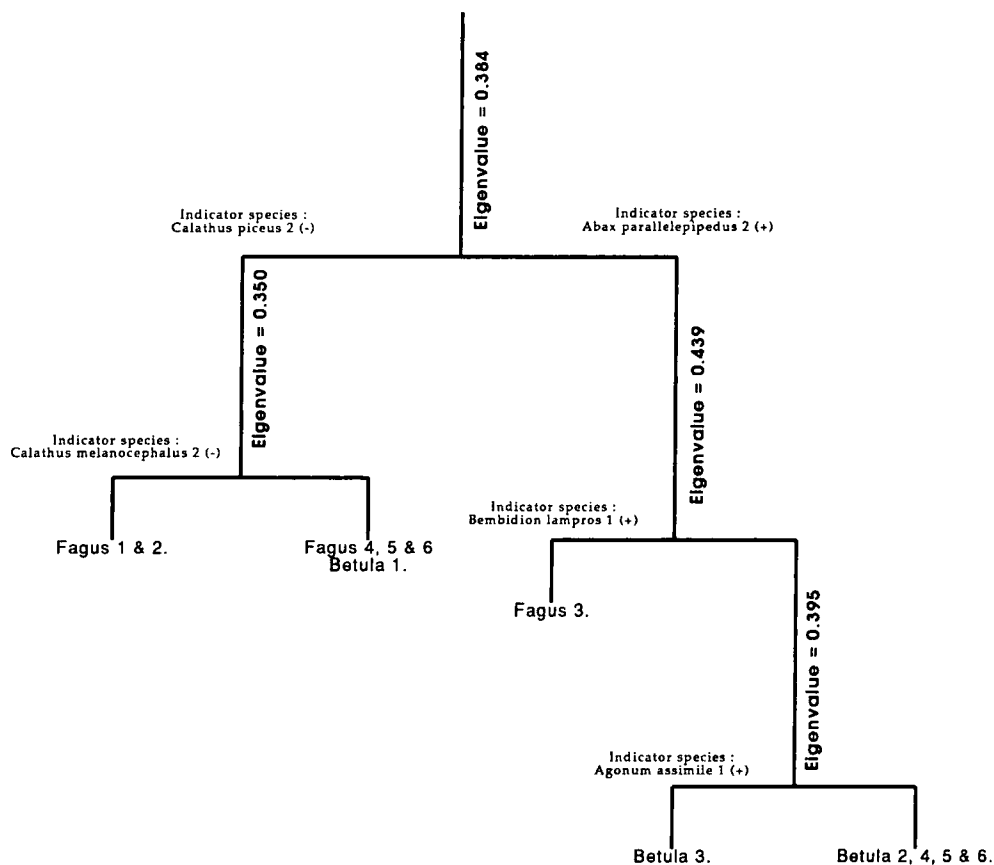
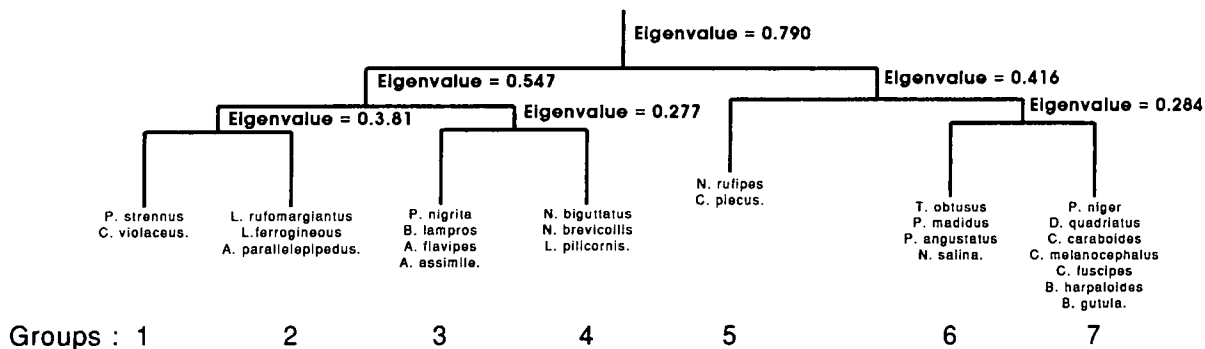


Figure 10. Twinspan classification of carabid species, sampled at High Beach, Epping forest.



**Table 5. Carabid species contingency table, based on percentages of individuals recorded at all Fagus and Betula sites, data sampled at High Beach, Epping forest,**  
N.B. not all species recorded in the present study are displayed here.

<div> <div>Carabid species :</div> <div>Categories :</div> </div>	Carabus violaceus	P. strenuus	Abax parallelepipedus	Leistus ferrugineus	L. rufo-marginatus	Pterostichus nigrila	Agonum assimile	Asaphidion flavipes	Bembidion lampros	Nebria brevicollis	Notiophilus biguttatus	Loncica pilicornis	C. piceus	N. rufipes	N. salina	P. angustatus	P. madidus	Trechus obtusus	B. gutula	B. harpaloides	Calathus fuscipes	C. melanocephalus	Cychrus caraboides	Dromius quadrimaculatus	P. niger
	Betula	16.1	0.9	37	1.6	1.5	1.2	0.6	0.7	0	14.7	5.7	1.4	11.2	2.1	2.4	0	2.1	0	0	0	0.9	0	0	0
Fagus	0.5	0	2.9	0.2	0.2	0.4	0.7	3.5	4.7	25.8	11.8	3.6	29.3	2.5	2.3	0.8	1.0	0.6	0.5	1.3	0.2	6	0.2	0.3	0.2
Betula/Fagus ratio.	32.2	-	12.8	8	7.5	3	0.9	0.2	-	0.6	0.5	0.4	0.4	0.8	1.1	-	2.1	-	-	-	-	0.2	-	-	-
TWINSPAN species class.	1	1	2	2	2	3	3	3	3	4	4	4	5	5	6	6	6	6	7	7	7	7	7	7	7

## DCA

The TWINSpan classification, showed distinct divisions between the *carabids* sampled in the *Fagus* and the *Betula* stands. The influence of environmental factors on the *carabid* distribution was analysed with the use of CANOCO but firstly a DCA ordination was run to visualise the distribution of sites and species, without the constraining effect of the environmental variables.

Figure 11 shows a DCA plot of the study sites according to the *carabid* data. This shows the *Betula* sites largely confined to the bottom left hand corner of the plot, the *Fagus* sites are spread over the rest of the graph.

In contrast with the DCA of the sites produced using invertebrate data, in which the *Fagus* sites were confined to a relatively small area and the *Betula* were spread over a wide area, the *carabid* DCA describing sites shows the opposite. The invertebrate data can inevitably only give general insights but the species identification of the *carabid* data enables the interpretation of a DCA plot to be a little more exact. It suggests a greater habitat heterogeneity amongst the *Fagus* sites than amongst the *Betula* sites and this is reflected in the presence of different *carabid* species.



Figure 11. DCA plot of the sample sites according to the *carabid* data, collected at High Beach, Epping Forest

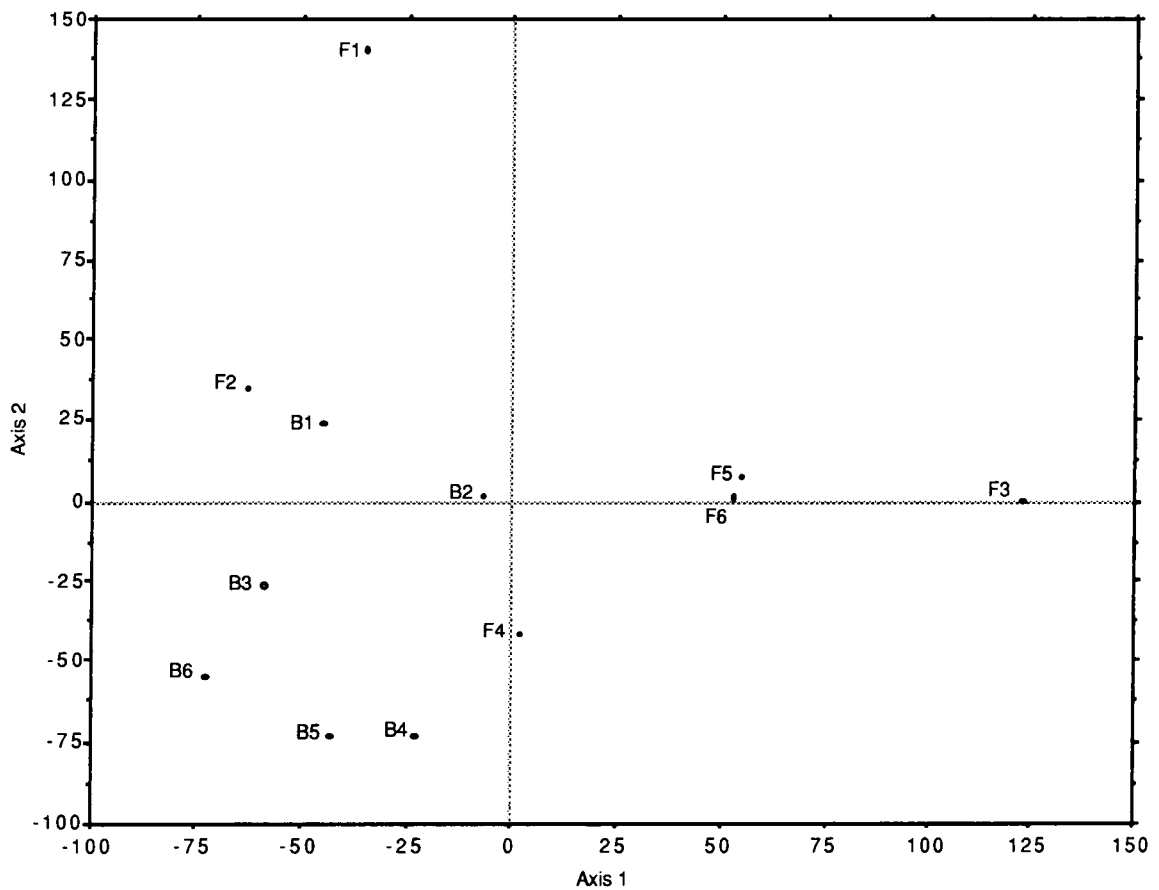
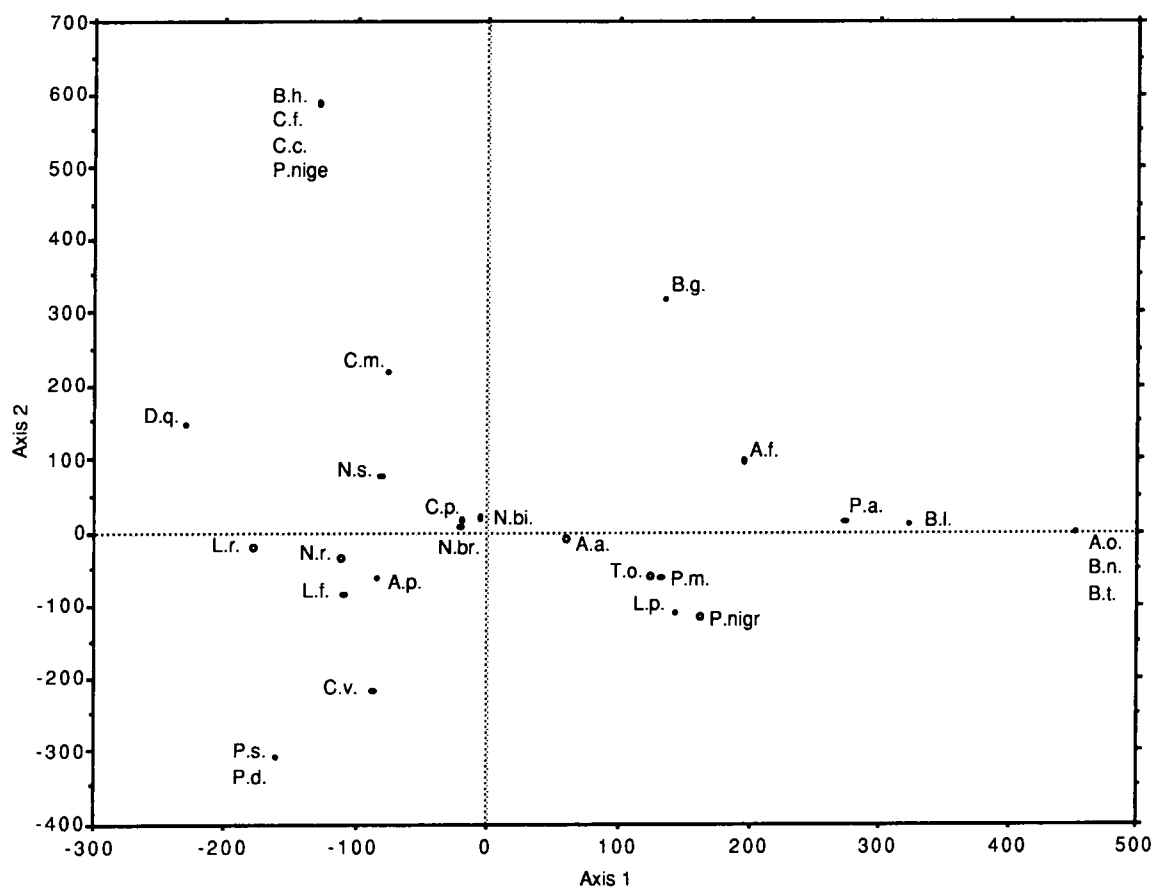


Figure 12 shows the DCA plot of the carabid species. The data in Table 3 assist the interpretation of the plot. Hence, *Carabus violaceus* (*Betula/Fagus* ratio 32.2), *Abax parallelepipedus* (12.8), *Leistus rufomarginatus* (7.5) and *L. ferrugineus* (8.0) etc. are mainly *Betula* inhabiting species and so they are mainly found in the bottom half of the plot. On the other hand, *Calathus piceus* (0.4), *Nebria brevicollis* (0.6) and *Notiophilus biguttatus* (0.5) are species mostly found amongst the *Fagus* and were recorded abundantly, thus they are positioned in

the centre of the graph. Special note must be made of *Agonum obscurum*, *Bembidion nitidulum*, *B. tetracolum* & *B. harpaloides*, *Calathus fuscipes*, *Cychrus caraboides* and *Pterostichus niger*, which were collected at *Fagus* sites 3 and 1 respectively. Table 5 shows that these species had a low percentage occurrence and this contributes to these sites being outliers on the plot.

Figure 12. DCA plot of the *carabids*, according to the data collected at High Beach, Epping Forest.



KEY : A.p. = *Abax parallelepipedus*, A.a. = *Agonum assimile*, A.o. = *A. obscurum*, A.f. = *Asaphidion flavipes*, B.g. = *Bembidion gutula*, B.h. = *B. harpaloides*, B.l. = *B. lampros*, B.n. = *B. nitidulum*, B.t. = *B. tetracolum*,

C.f. = *Calathus fuscipes*, C.m. = *C. melanocephalus*, C.p. = *C. piceus*, C.v. = *Carabus violaceus*, C.c. = *Cychrus caraboides*, D.q. = *Dromius quadrinotatus*, L.f. = *Leistus ferrugineus*, L.r. = *L. rufomarginatus*, L.p. = *Loricera pilicornis*, N.br. = *Nebria brevicollis*, N.s. = *N. salina*, N.bi. = *Notiophilus biguttatus*, N.r. = *N. rufipes*, P.a. = *Pterostichus angustatus*, P.d. = *P. diligens*, P.m. = *P. madidus*, P.nige. = *P. niger*, P.nigr. = *P. nigrita*, P.s. = *P. strenuus*, T.o. = *Trechus obtusus*.

## CCA

The environmental variables used in the invertebrate CCA were used in a CCA carried out on the *carabid* species. Table 6 and 7 show the results for axis 1 and 2 respectively.

Table 6. Results of a CCA *carabids* for the 1st axis, from data collected at High Beach, Epping Forest.

Environmental variable	Regression coefficients	t-values	Inter-set correlations
Leaf litter water content	- 292	- 862	- 903
Light	- 103	- 351	- 602
Vegetation cover	- 123	- 457	- 614
Ground Temperature	- 181	- 500	- 832

Table 7. Results of a CCA *carabids* for the 2nd axis, from data collected at High Beach, Epping Forest.

Environmental variable	Regression coefficients	t-values	Inter-set correlations
Leaf litter water content	332	353	264
Light	- 156	- 192	- 497
Vegetation cover	198	266	459
Ground Temperature	- 393	- 391	- 453

N.B. the values in these tables have been multiplied by 100

The water content of the leaf litter was the most important variable influencing axis 1 ( $p < 0.06$ , Monte Carlo permutation test). This result was a little surprising considering the t-values and the inter-set correlations. Of secondary importance is the ground temperature. Figure 13 shows the plot of sites according to *carabid* data. *Betula* site 1 is most like the *Fagus* sites, this is probably because it is a very small stand (approximately 10 x 10m). The influence of the surrounding *Fagus* must be too overwhelming for the stand to demonstrate a *carabid* assemblage typical of most *Betula*. Many of the trapped specimens are probably touristic species which happened to wander in from the encompassing *Fagus* stand. Further, *Betula* site 1 being such a small corpse of trees is not substantial enough to accumulate a significant leaf depth (which is co-variable with the water

content of the leaf litter and probably a causative factor). The presence of *Betula* site 1 in the *Fagus* groupings has already been explained and apart from *Fagus* site 1 (which will be dealt with latter), the whole plot bisects the *Betula* from the *Fagus* sites, along two pairs of major gradients. The *carabids* in the *Betula* stands are showing a preference for the high humidity associated with leaf litter and vegetation cover, whilst the *carabids* in the *Fagus* stands are showing a preference characterised by high temperature and light intensity at ground level. *Fagus* site 1 differs from the other sites because of all the sites it is the second highest and is perched on a hillock. In conjunction with the fact that it has very little leaf litter, mean of 2.7 and a free draining fine sandy soil (after *Betula* site 1 it has the highest mean percentage mineral content of its soil at 43.5%), (see Appendix 2 and 5), it has a mean percentage water content of its leaf litter of 21.4, lowest of all the sites. Equally of interest is that *Fagus* site 1 has the lowest mean percentage light intensity of all the *Fagus* sites, with 37.3 and the lowest mean ground temperature of all the *Fagus* sites, with 17.9. It is thus reflected so by the distribution of a few rare *carabids* when presented in this ordination plot. The CCA plot for the *carabids* can be seen in Figure 14.

Figure 13. CCA plot of the sample sites according to the *carabid* data, collected at High Beach, Epping Forest (the arrows represent the strength and direction of environmental gradients).

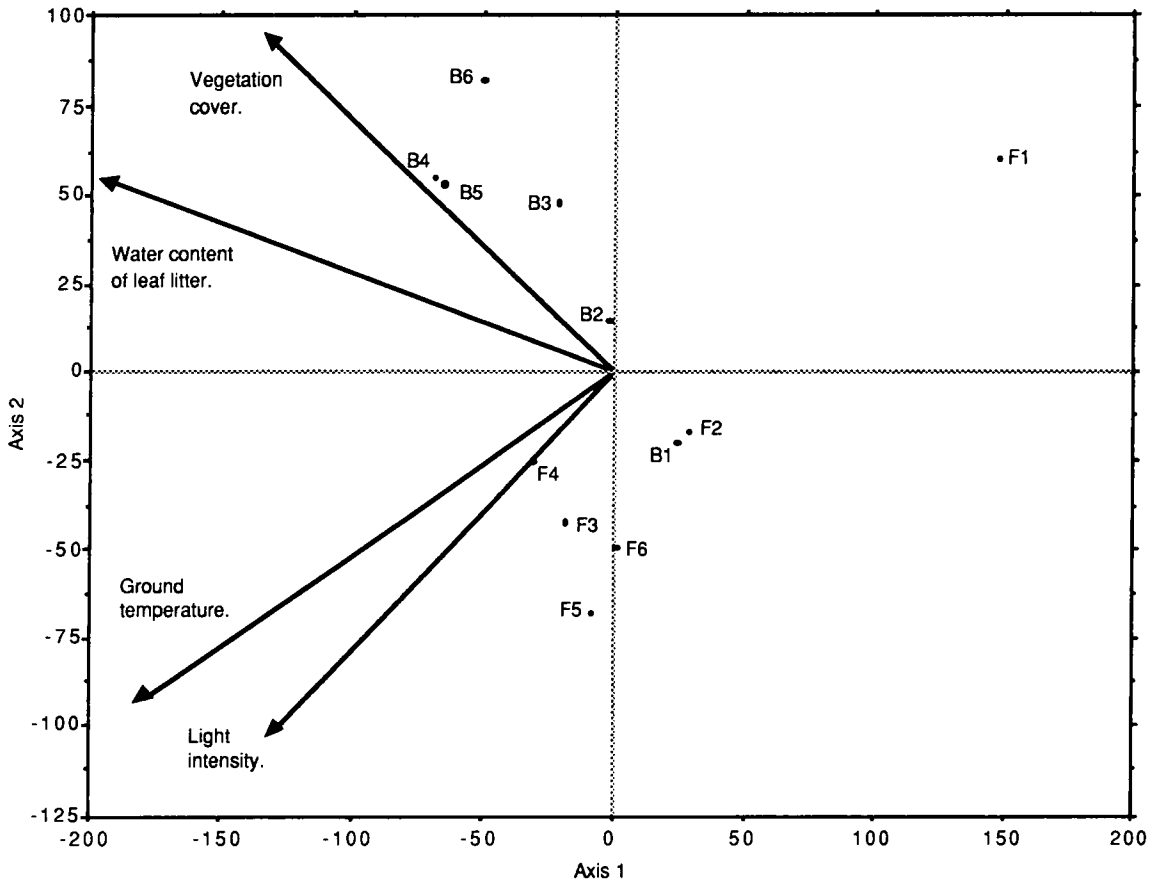
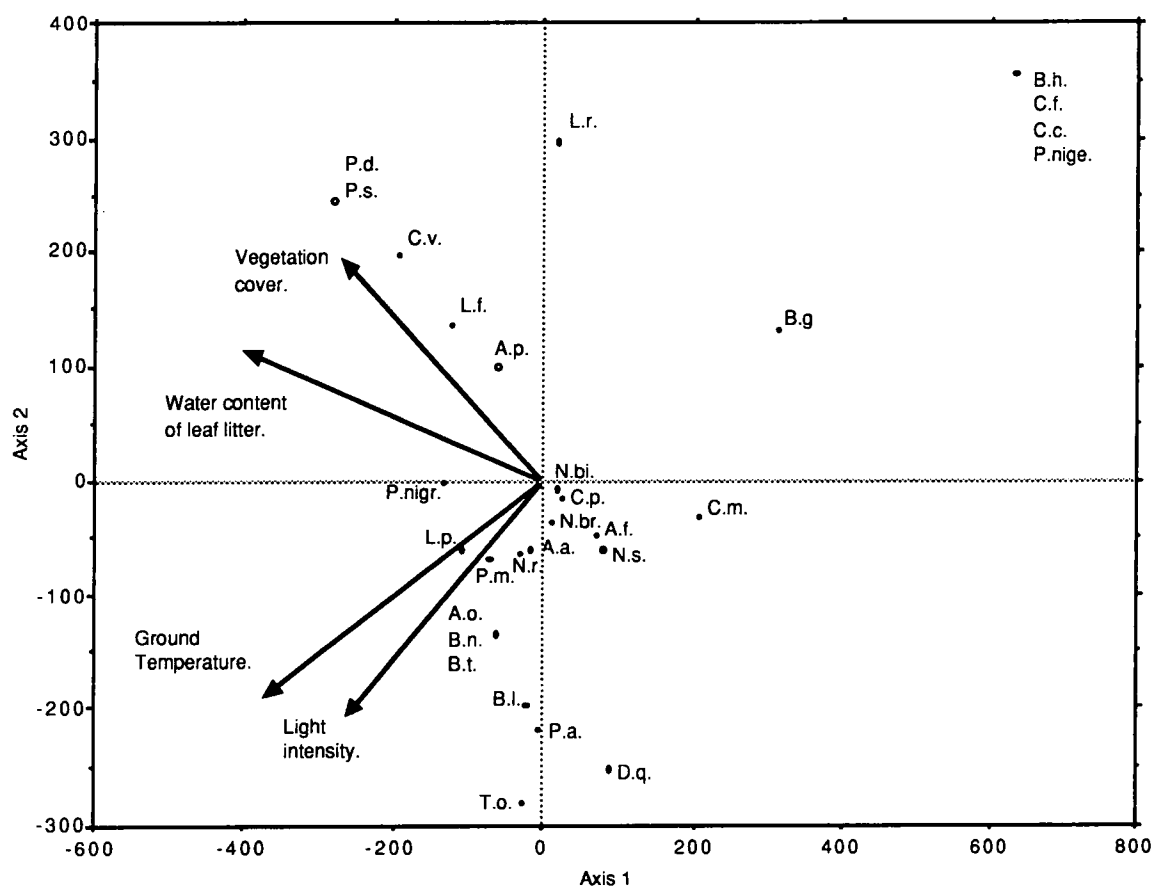


Figure 14. CCA plot of the *carabid* species according to data, collected at High Beach, Epping Forest.



KEY : A.p. = *Abax parallelepipedus*, A.a. = *Agonum assimile*, A.o. = *A. obscurum*, A.f. = *Asaphidion flavipes*, B.g. = *Bembidion gutula*, B.h. = *B. harpaloides*, B.l. = *B. lampros*, B.n. = *B. nitidulum*, B.t. = *B. tetracolum*, C.f. = *Calathus fuscipes*, C.m. = *C. melanocephalus*, C.p. = *C. piceus*, C.v. = *Carabus violaceus*, C.c. = *Cychrus caraboides*, D.q. = *Dromius quadrinotatus*, L.f. = *Leistus ferrugineus*, L.r. = *L. rufomarginatus*, L.p. = *Loricera pilicornis*, N.br. = *Nebria brevicollis*, N.s. = *N. salina*, N.bi. = *Notiophilus biguttatus*, N.r. = *N. rufipes*, P.a. = *Pterostichus angustatus*, P.d. = *P. diligens*, P.m. = *P. madidus*, P.nige. = *P. niger*, P.nigr. = *P. nigrita*, P.s. = *P. strenuus*, T.o. = *Trechus obtusus*.

From Figure 14, it appears that *A. parallelepipedus*, *Carabus violaceus*, *Leistus ferrugineus*, *Pterostichus diligens* and *P. strenuus*, are mainly *Betula* inhabiting species and are positively affected by the vegetation cover and water content of the leaf litter. Whilst *Notiophilus rufipes*, *Loricera pilicornis*, *P. madidus*, *P. angustatus* and *Bembidion lampros* are species mostly found amongst the *Fagus* and seem positively affected by Light intensity and Ground temperature.

### Stepwise Multiple Regression

The CCA showing the position of individual *carabid* species shows affinities of different species to the environmental variables. Such information can then be used to predict species abundance by using a stepwise multiple regression to obtain a predictive equation. The abundant species were used and the significant results are shown in Table 8. In each case only one of the five environmental variable was significant. Comparison with the original CCA plot confirms the trends between the abundance of each species and the variable to which they were correlated by the stepwise multiple regression.

Table 8. Results of a stepwise multiple regression on selected carabid species, using environmental factors determined as important with the use of a CCA, from data collected at High Beach, Epping Forest.

Species	Environmental variable	Constant	B value	r value	't' value	Sig t
<i>L. pilicornis</i>	Ground temperature	- 5.5	0.3	0.8	4.2	0.002
<i>N. brevicollis</i>	Leaf litter water content	6.0	- 0.1	- 0.7	- 2.8	0.020
<i>N. biguttatus</i>	Leaf litter water content	2.4	0.1	- 0.6	- 2.4	0.036
<i>C. piceus</i>	Leaf litter water content	6.3	- 0.1	- 0.6	- 2.5	0.034
<i>C. violaceus</i>	Vegetation cover	- 0.1	0.1	0.9	5.4	0.003

## Discussion

### The major invertebrate groups at High Beach, Epping Forest

Describing the distribution of the major invertebrate groups at High Beach, Epping Forest is not the prime objective of the present study and so only limited space is allocated here. The CANOCO results suggest that the major invertebrate groups are mostly influenced by a humidity gradient and by vegetation cover. Humidity appears to positively affect the *Opiliones* and *Isopoda* the most and the *Carabidae*, *Coleopterous larvae* and the *Dermaptera* the most negatively, these results are not unexpected as all invertebrates are prone to the dangers of dessication. Vegetation cover seems to positively affect *Hymenoptera* and the *Araneae*. The *Hymenoptera* may be searching the vegetation for prey (as would be the case with the many parasitic wasps recorded) or they may be collecting pollen and nectar from the brambles (*Rubus fruticosus*) flowers, in the case of bumble bees. The many *Araneae* may be using the vegetation for the structural support of their webs. The absence of vegetation cover appears to be most favourable to the *Carabidae* and the *Coleopterous larvae*, both these groups would be mostly hunting in the open and vegetation would no doubt restrict their freedom of movement and field of vision. The *Dermaptera* are a group positively influenced by light. They are opportunists and no doubt search the open bright areas for food, where competition is not so intense. The CANOCO results for the *Carabidae* suggest that in comparison with the other invertebrates the *Carabidae* prefer dry, vegetation free habitats, with little leaf litter and medium light intensities.

### *Carabid* assemblages

Most ecologists look at *carabid* assemblages calling them communities and Den Boer (1986a), made it clear that in most cases the functional interaction and relationships which are the property of a true community are lacking. For the purposes of this study, the definition of a *carabid* community is to be considered in the same light as that expressed by Butterfield and Coulson (1983), "as an assemblage of species which recurs at a number of sites and no further properties are implied".

### *Carabid* niche

Thiele (1977), describes the *carabid* niche as comprised by mainly predatory



arthropods, that hunt their prey on the ground and consume considerable quantities of carrion and plant matter. This holds true of the adults only. This study looks specifically at woodland *carabids* and Greenslade (1965), suggested that *carabids* in woodland habitats are mostly nocturnal, with larvae in the winter and a period of adult activity in the late summer (mainly for copulation). Further he determined (1964) that densities of *carabids* within woodlands were significantly lower than in other habitats (*Fagus* woodland 1.33 per m<sup>2</sup>). In the present study most of the *carabids* recorded in the *Fagus* stands were probably diurnal, whilst those of the *Betula* stands were probably nocturnal. In a classification and ordination of habitats of *carabids* in the North-East of England (Luff, Eyre and Rushton 1989) twenty of the species recorded in the present study, were characterised as woodland dwelling species.

### **Classification and ordination of *carabid* assemblages**

A number of authors have classified *carabids*, mostly with the use of TWINSpan, for example Eyre and Luff (1990), and Luff, Eyre and Rushton (1989) but also cluster analysis, Butterfield and Coulson (1983). Gauch (1986), suggested that multivariate techniques can be used as a tool giving new insights into the patterns hidden within data sets that may not be readily visible with the use of other statistical procedures. The benefits of classification methods may be dubious but apart from the assemblages they help identify, Butterfield (1987), has suggested that the indicator species produced by TWINSpan may be of use to assess the status of *carabid* assemblages for conservation purposes. There can be little doubt that ordination techniques are much more revealing as Eyre and Luff (1990), Luff (1990a) and Maelfait and Desender (1990) have shown, because they can easily be related to environmental variables.

Both classification and ordination techniques were used in the present study and these helped elucidate the distribution of various *carabid* assemblages and the major environmental factors governing their distribution within the woodland ecosystem.

### **Population dynamics of *carabid* assemblages**

Den Boer (1985), suggested that woodlands or "old forests" form permanent habitats, but that they do not form stable habitats for *carabids* "apparently mean survival times of local populations only rarely exceed 100 years". Thiele (1977), notes that microclimate of forests/woodlands play an essential role in

determining the distribution of *carabids*, suggesting that woodland *carabids* "are almost all very hygrophilic and show little resistance to dryness" this is in sharp contrast with open country species. Equally woodland species almost exclusively prefer the dark and shady areas.

Greenslade (1961), found a correlation between temperature and activity and concluded (1964a) that although high temperatures may be favourable to the *carabids*, the low humidity associated with such phenomena is not.

Hence, in woodlands which show both closed and open canopy conditions, one might expect distinct *carabid* communities to exist.

At High Beach, Epping Forest the hurricane winds of the late eighties toppled many of the great pollarded *Fagus*, temporarily leaving a clearing for colonisation by a different species set of *carabids*, before a *Betula* stand could take root. To be able to respond to such a change *carabids* must have a swift dispersal mechanism. Thiele (1977), comments that "*carabids* are capable of movement on the ground and that their distribution over wide areas appears to be possible without flight".

Den Boer (1981), found that individuals of *Calathus melanocephalus* (a species recorded in the present study) travelled 40 - 80 metres between trapping sessions. He notes that higher densities of one *carabid* species compared to another in the same habitat, are apparently of only little value for survival. What appears to be most important is that a species has a population spread over a wide area. In some parts of this network of "interaction groups" population densities will be higher than in other areas. This implies that even species with rather poor powers of dispersal would easily repopulate (mainly by immigration) a depopulated site when conditions become favourable. At High Beach, Epping Forest, this is indicated by the differences in species abundance (Figure 8), which is a snapshot view for only one sample season and would be expected to change from year to year. Den Boer (1985), classifies species as either T-species (with high powers of dispersal) or L-species (with low powers of dispersal). His work suggests that local populations of *carabids* survive for only restricted periods, T-species around 10 years and L-species 40 years.

The work of Atkinson *et al.* (1987) has demonstrated that fossil assemblages of *coleoptera* (mainly *carabids*) responded very quickly to climatic changes. Den Boer's ideas help explain such phenomena. Evidently the species assemblages of different "interaction groups" are not only dynamic and in constant fluctuation

with the environment, but as a consequence extremely ephemeral in different spatial locations.

Luff (1990a) in his work on the stability of *carabid* communities concurs with Den Boer and observes that some of the least stable populations are those with the greatest powers of dispersal by flight. In his study he found that the principle axis of variation was attributable to the fluctuation in numbers from year to year. "As a consequence of this process" Den Boer argues "it may be expected that local populations of *carabids* become extinct rather quickly. Although such extinctions may be of a temporary nature. It seems that in the temporal sense the abundance of *carabid* populations fluctuate in their amplitude, as the environmental constraints in operation on the assemblages shift and change. Butterfield and Coulson (1983) note "the numbers of species and individuals caught as well as the species composition, differ between communities". Den Boer's theory of dynamic assemblages of fluctuating interaction groups helps us understand Butterfield and Coulson's observation.

Den Boer suggests that "as probably no organism can completely withdraw itself from the vagaries of its physical environment, unpredictable changes of the physical environment will necessarily result in fluctuations of population numbers".

### **Factors affecting *carabid* distribution**

Evans (1983), introduces the double sided concept of *carabid* habitat selection. "Responses to olfactory stimuli associated with soil microorganisms help *carabids* locate their habitats, while kinetic responses to microclimatic factors within the habitat serve to maintain favourable body temperatures and regulate timing of their various activities". Unwin and Corbet (1991), make the reader infinitely aware of how strictly invertebrate behaviour and distribution is governed by microclimatic factors. For each *carabid* species, different environmental factors appear to be of greater importance than others. Thiele (1977), observes that *Agonum assimile* (a species recorded in the present study) prefers to seek an optimum temperature, rather than its optimum humidity. Many workers have undertaken experimental work to determine the tolerance limits of different *carabid* species to various environmental factors, Thiele (1977) reports these to a large extent, but cites Lindroth (1949), "The experiments represent an attempt to isolate the external factors acting upon the animal in nature and to estimate their influence. However, the very isolation of such factors is an unnatural process. We

cannot, for example claim to know the absolute temperature preference of a particular species since this simply does not exist ; it depends, amongst other things, upon air humidity....". Further Thiele notes that "an experiment can show that there is no correlation between a species and an environmental factor to which the species appears to be correlated to in the field. The conclusion is then justified that the distribution of the species is not influenced by this factor, but either by another or several others which vary in parallel with the first".

The present study has not involved laboratory experimentation, but the search for co-variation amongst the 18 environmental variables was recorded using Pearson correlation. By adding and removing different variables CANOCO can help determine the most significant choices. Whilst the "best" variables were chosen using this method it must be remembered that the rejected co-variables could still be the more important and only continuous recording of these variables or/and an experimental approach may reveal the truth.

From comprehensive experimentation Thiele produced a comparative table for temperature, humidity and light preference of different *carabid* species. From that table, those species recorded by the present study have been extracted and can be seen in Table 9.

Table 9. Classification of those *carabid* species recorded in the present study, according to their preference of temperature, humidity and light, based on the work of Thiele (1977). The term Cold/Warm or Wet/Dry suggests an intermediate between Cold or Warm, Wet or Dry etc.

Species	Temperature	Humidity	Light
<i>Pterostichus niger</i>	Warm	Wet	Dark
<i>Calathus piceus</i>	Warm	Wet/Dry	Dark
<i>Nebria brevicollis</i>	Warm	Wet/Dry	Dark
<i>Agonum assimile</i>	Cold	Dry	Dark
<i>Nebria salina</i>	Cold	Wet/Dry	Dark
<i>Carabus violaceus</i>	Cold/Warm	Wet/Dry	Dark
<i>P. nigrita</i>	Cold/Warm	Wet/Dry	Dark
<i>P. angustatus</i>	Cold/Warm	Dry	Dark
<i>Calathus fuscipes</i>	Cold/Warm	Dry	Dark
<i>Abax parallelepipedus</i>	Cold/Warm	Wet	Dark
<i>Bembidion tetracolum</i>	Cold/Warm	Wet	Dark
<i>P. madidus</i>	Cold/Warm	Wet	Dark/Bright
<i>Asaphidion flavipes</i>	Cold/Warm	Wet/Dry	Dark/Bright
<i>Loricera pilicornis</i>	Cold	Wet/Dry	Bright

The species are mostly species which prefer dark conditions and it is possible that as a whole this environmental factor characterises woodland *carabids* the most and possibly the reason why light turned out to be the third most important variable as determined by the CANOCO in the present study.

However, Thiele's results do not concur with those determined by CANOCO in the present study. For example, in the present study *Abax parallelepipedus* shows preference for moist habitats and therefore reflects Thiele's results but the other species do not appear to be consistent. Perhaps, Thiele's general comparative table is too coarse to compare with that of this study, which must by its scale, be looking at a narrower spectrum of variation.

Both Thiele (1977) and Rushton, Luff and Eyre (1989), suggest that the presence of plant cover does not affect the distribution of *carabids*, again the present study does not agree with this assessment. This may be because in the present study it was deliberately decided to choose at the onset sites with and without vegetation cover. Stepwise multiple regression of the abundance of *Carabus violaceus* against the five most important variables determined by CANOCO, gave a significant results, selecting vegetation cover as the principle factor predicting *Carabus violaceus* abundance (Table 8).

Further Greenslade (1964a), suggested that ground vegetation may impede *carabid* movement and so reduce the pitfall catch. It is possible that Greenslade was indirectly measuring microclimatic changes produced by vegetation structure and that it was these changes that were affecting the *carabid* abundances in the pitfalls. Maelfait and Desender (1990), identified groups of *carabids* that appeared to occur in woodlands where they found situations with fast litter breakdown. Greenslade (1964b), found an inverse relationship between the abundance of *Nebria brevicollis* and leaf litter depth. Later Greenslade (1965) suggested that the richest *carabid* fauna was found where litter development was least. This concurs with the present study as shown by the pitfall catch, where the leaf litter depth at different sites was co-varying with the principle gradient picked out by CANOCO, which was the water content of the leaf litter.

The stepwise multiple regression (Table 8) for the abundance of *Calathus piceus*, *Nebria brevicollis* and *Notiophilus biguttatus* gave a direct positive relationship with the water content of the leaf litter. Perhaps Greenslade's results in themselves reflect humidity gradients. Thiele (1977), suggests that soil factors

have little influence on the distribution of *carabid* species. Appendix 2 illustrates that the soil conditions were very similar from one site to the next at High Beach and so it was not to be expected that any differences would be seen.

However, Thiele does point out that in forests on acid soil the air layer near the ground, is subject to greater fluctuations in moisture and temperature. At High Beach, Epping Forest, the soil pH co-varied with leaf depth (Table 2). Eyre and Luff (1990a), found that in a classification of European grassland habitats, using *carabids* soil water was an important factor in the distribution of *carabid* assemblages. The water content of the leaf litter and soil water could both be described as humidity and the work discussed so far points to humidity being the most important factor.

Butterfield and Coulson (1983) concluded that the most important factors affecting the distribution of *carabids* would be soil water content, vegetation height and temperature. The present study identifies humidity, light and thus temperature at ground level and vegetation cover as the most important factors. Thus the present study is in general agreement with other authors.

### ***Carabid* body size and feeding strategies**

Many workers have looked at body size of *carabids* with the view that it may impede movement in the vegetation : Luff (1990a), Greenslade (1964), Baars (1979), and thus affect pitfall results. Rushton, Luff and Eyre (1991), suggest that large generalist *carabids* can utilise a greater width of the available food source spectrum, than can small generalist species. If this is true then one would expect body size to be related to the differing feeding strategies of the species concerned. The present work has revealed evidence to support this theory. With the use of the *Betula/Fagus* ratio of the percentage abundance of different *carabid* species at these stands (Table 5), a table can be compiled to show the apparent relationship between mean body size (in accordance with Lindroth 1985-86) and the distribution of species abundance at *Betula* and *Fagus* sites, (Table 10).

Table 10. A table of the *carabid* species recorded by the present study, classified in accordance to mean body size mm (Lindroth 1985-86), dietary class (Forsythe 1982, 1987, Penny 1966 and Luff 1974) and *Betula*/*Fagus* ratio as determined at High Beach, Epping Forest.

Species	<i>Betula</i> / <i>Fagus</i> ratio	Mean body size (mm).	Dietary class
<i>Carabus violaceus</i>	32.2	25	Scavenger
<i>Abax parallelepipedus</i>	12.8	20	Scavenger
<hr/>			
<i>Leistus ferrugineus</i>	8	7.25	Carnivore
<i>L. rufomarginatus</i>	7.5	8.75	Carnivore
<hr/>			
<i>Pterostichus nigrata</i>	3	10.8	Omnivore
<i>P. madidus</i>	2.1	15	Omnivore
<i>Nebria salina</i>	1.1	11.75	Carnivore
<i>Agonum assimile</i>	0.9	10.5	Omnivore
<hr/>			
<i>Notiophilus rufipes</i>	0.8	6.05	Carnivore
<i>Nebria brevicollis</i>	0.6	12	Carnivore
<i>Notiophilus biguttatus</i>	0.5	5.5	Carnivore
<i>Calathus piceus</i>	0.4	9.5	Carnivore
<i>Loricera pilicornis</i>	0.4	7.25	Carnivore
<i>Calathus melanocephalus</i>	0.2	7.4	Carnivore
<i>Asaphidion flavipes</i>	0.2	4.3	Carnivore
<i>Bembidion lampros</i>	-	3.7	Carnivore

N.B. The rare species occurring at only *Betula* or *Fagus* stands have been omitted from this table with the exception of *Bembidion lampros*, which is reasonably common on the *Fagus* sites.

The trend is for the very large species to inhabit the *Betula*, the middle sized species to inhabit both stands, while the smaller species (including all species of *Bembidion*) mostly inhabit the *Fagus* stands (c.f. Figure 8).

Many authors, Den Boer (1986b), Thiele (1977), etc. suggest that competition maybe of little importance in determining *carabid* distribution. However, Lenski (1982, 84), undertook experiments on two *Carabus* species which produced evidence for competition for food between the two species.

Table 10, also shows the dietary status of the different species, based on the work of Forsythe (1982, 87), Penny (1966) and Luff (1974). This suggests that the majority of *carabids* are small to medium sized species, living mostly in the *Fagus* (and are mostly carnivorous), such as *Bembidion lampros*, *Asaphidion flavipes* and *Notiophilus biguttatus*. The few large species such as *Carabus*

*violaceus*, *Abax parallelepipedus*, *Pterostichus nigrita* and *P. madidus*, live mostly in the *Betula* (and on the whole are either omnivores actively hunting or scavengers looking for carrion). This doesn't fit well with the work of Dawson (1965), in which she found all the small *carabids* were catholic feeders but that was a fenland study and the environment at High Beach is very different. Wheeler (1988), found that although the sizes of prey eaten overlapped among *Pterostichini* of different sizes, there was a direct correlation between the distance of the mandibles at full gape and the median sizes of prey attacked, for *Pterostichus madidus*, *P. melanarius*, *P. niger*, *P. nigrita* and *Abax parallelepipedus*, ( $r^2 = 0.95$ ,  $t = 5.13$ ,  $p = 0.014$ ). All except *P. melanarius*, were recorded in the present study. Wheeler suggests that ease of capture restricts the prey sizes taken by smaller predators, giving larger species a greater range of potential prey, thus agreeing with Rushton, Luff and Eyre (1991).

The observations set out here suggest that larger *carabids* search for a wide range of food types within the *Betula* stands and the smaller species in the *Fagus* stands have a narrower range to choose from. Since prey size would seem to be important, it is appropriate to look at the captures of other invertebrates at the *Betula* and *Fagus* sites.

Firstly, the total mean abundance of invertebrates as shown by the pitfall catch was greater in the *Betula* (10.5), than it is in the *Fagus* (6.1) and Secondly, it is clear from Figure 1 that large invertebrates such as *Opiliones*, *Araneae*, other *Coleoptera*, *Diptera*, *Hymenoptera* and *Isopoda* are all more abundant in the *Betula* sites than in the *Fagus* sites. Evidentially the *carabids* in the *Fagus* stands must be mostly feeding on springtails and mites.

Forsythe (1987), suggested that there may be a relationship between eye size and feeding strategy. For example, *Notiophilus biguttatus*, *Asaphidion flavipes*, *Bembidion lampros* all have relatively large eyes in relation to their body size, whilst *Abax parallelepipedus*, *Carabus violaceus* and *Pterostichus madidus* have eyes that are small in relation to their body size. The former species, found in *Fagus*, are small species and are active hunters, whilst the latter species, found in *Betula*, are large species and omnivores or scavengers. Such feeding strategies also suggest that the majority of *carabids* that live in the *Fagus* sites are probably diurnal (and the author of the present study has found this to be so during experiments to estimate population size, using the same method). Whilst the species found in the *Betula* sites are probably nocturnal (no characteristic



species being found whilst using the white tray method).

The CANOCO results for the *carabids* (Figure 14) suggest that those species found in the *Fagus* sites prefer higher ground temperature and light.

The species found in the *Betula* sites are mostly influenced by humidity and vegetation cover.

Whilst, Thiele (1977), gives an example of behaviour causing the different distributions of *Abax parallelus* and *A. ater*, little behavioural work has been done with *carabids* and so it is difficult to say with any certainty that behavioural effects can account for this size difference between the *Fagus* and *Betula* sites but if the small *carabids* are mostly active hunters their behaviour will be dictated by the vagaries of the surrounding temperature. *Fagus* sites being generally more open to the light are as a consequence warmer, are habitats that accommodate hunters searching for springtails and mites, on a simply structured substrate.

The *carabid* scavengers of the *Betula* sites are more dependent on finding carrion and so they do not have to modify their behaviour to actively absorb as much solar radiation in order to be fast and efficient hunters, they no doubt detect their food via chemical attractants. Hence, the distribution of the large *carabids* will reflect the distribution of the majority of the invertebrate groups, since the most carrion will be found where the greatest number of invertebrates are. Thus, the invertebrates as a whole and the large *carabids* will share similar responses to environmental gradients.

In both cases the major invertebrate groups and the large *carabids* found in *Betula* sites, the two most important environmental gradients as described by CANOCO are humidity and vegetation cover (Tables 3 & 4 and Figure 14).

The notable exception to these ideas are the two *Leistus* species found in the *Betula* sites. They do not depend on good eyesight to hunt, having very small eyes in relation to their bodies, but are tactile hunters, preferring deep leaf litter and using their seatal cages to trap leaf litter inhabiting springtails and mites, Forsythe (1987). This special adaptation to an unusual habitat for carnivorous hunting *carabids*, is no doubt partly the answer for the recent spread of *Leistus rufomarginatus* which has only recently colonised Britain, Crowson (1942).

### **The effect of vegetation on microclimate**

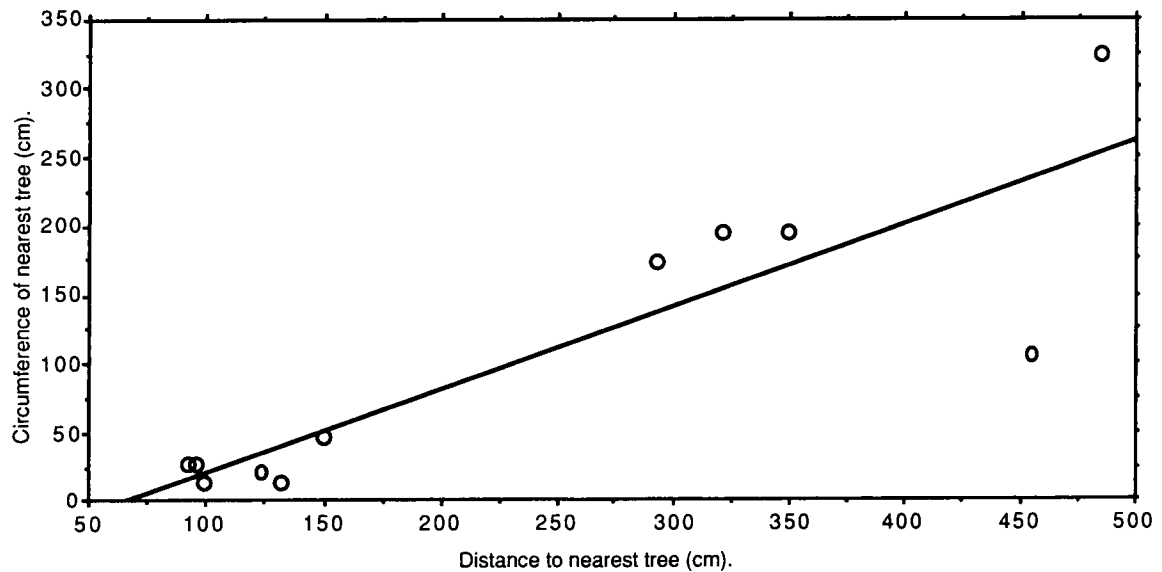
So far the major factors affecting the distribution of different *carabids* at different sites has been discussed and reasons for why such factors are important have

been suggested. The next link in this chain of causality is to consider what causes variation in these environmental factors. Such an understanding being most useful in the application of the ideas discussed so far, for conservation aims. Luff (1965), carried out interesting work on the microclimate of *Dactylis glomerata* and found that during warm sunny weather the microclimate remained stable inside the *Dactylis* tussocks in comparison with grass that grew with a more open structure. During cloudy cold days the difference was not so great and after snow fall, the tussocks were insulated and so kept a higher temperature than the surrounding vegetation. Further, Luff (1966), examined the *coleopterous* fauna of these tussocks and his studies lead him to conclude that there was a "need for a detailed classification of microhabitats" which themselves would be greatly affected by microclimatic factors. Greenslade (1964b), recognised the importance of macroclimatic factors when he attributed population fluctuations of *Nebria brevicollis* which fell from 2300 in 1959 to 200 in 1960, to climatic factors.

At High Beach, Epping Forest the density of trees within the respective stands affects the distribution of *carabid* beetles in two ways: Firstly, the denser they are the greater the ability to retain leaf litter around their bases and secondly, the denser their canopy the darker will be the forest floor.

Measurements of the distance to the nearest tree (from each pitfall) and the size of the trees circumference were made during the field work (Appendix 5). There was a negatively proportional relationship between leaf litter depth and 1) the circumference of the nearest tree and 2) the distance to the nearest tree,  $r = -0.66$  ( $p < 0.02$ , d.f. = 11) and  $-0.68$  ( $p = 0.01$ , d.f. = 11) respectively. Further, the density (measured as the mean distance to the nearest tree) of the stands decreases with age (measured as the mean circumference of the nearest tree),  $r = 0.88$  ( $p = 0.001$ , d.f. = 11), Figure 16. Distance form one tree to another, or pitfall, being an inverse measure of density.

Figure 16. A scattergram of the mean distance to the nearest tree against mean circumference of the nearest tree, according to data, collected at High Beach, Epping Forest.  $R = 0.88$  ( $p = 0.001$ , d.f. = 11).



As the stands increase in age so their density decreases, as the density decreases so the break down of leaf litter increases. Ironically, the wind blows what is mostly *Fagus* leaf litter to the young *Betula* stands (Appendix 5). As part of the successional process the old, over-weighted crowns of the pollarded *Fagus*, which have been neglected for over 100 years, will eventually bring the tree down, with the appropriate catalyst, such as the hurricane winds of 1987 and 1990. Then the pioneer *Betula* will take hold and the leaf litter will start to accumulate. Rodwell (1991), supplies evidence that suggests *Betula* site 4 is a *Quercus/Betula* representative of a midway point in the successional process between pioneer *Betula* and mature *Fagus* woodland. If this is so, with regards to the *carabids*, it is not dissimilar to the other *Betula* sites. As the vegetational succession takes place, the dynamic assemblages of *carabids* (as explained by Den Boer's work) will be colonising new sites increasing and decreasing in abundance as and when the environmental gradients change. Hence, if left undisturbed the vegetational succession should be followed by a recognisable invertebrate succession. The results of the present study suggest that the richest

*carabid* fauna is to be found where leaf litter is least. However, as long as the pollards remain neglected, *Fagus* sites will continue to deteriorate and the open substrate that appears to be so essential a component of the active species environment, will diminish.

### **Applications of the present study for conservation management**

Over the past 100 years Epping Forest has suffered the fate of a fundamental paradox. Ranson (1978), makes this clear "When the Epping Forest Act laid down that the natural condition of the forest be maintained" an impossible task was set since "there was no natural condition to maintain". The intensive management of the woodland has played a central role in the economy of the Epping district. Every imaginable economic use was made of the forest, from the extraction of turf, gravel and timber to grazing and pannage activities. With the enforcement of the 1878 Epping Forest Act, this was discontinued. Because of the cessation of these intense activities, Rackham (1980), explained "The forest is now on the way to becoming undistinguished secondary woodland. Its distinctive features, the pollards, non-timber trees, shrubs and underwood are declining through neglect and excessive shade".

In order to assess the invertebrate communities of different localities Disney (1987), used vegetation types to characterise communities. The present study has avoided such an approach since many of the works cited in the present study have frequently shown that invertebrate assemblages are affected by numerous other environmental gradients. In woodland conditions it is the examination of such physical/chemical gradients (often the indirect product of vegetation management) that lead to an understanding of invertebrate distribution.

Eyre and Rushton (1989) have pointed out the political significance of rare species as flag species which draw the interest of the public. From the ecologist's point of view, rare species tell us very little. In the present study *Pterostichus angustatus* was discovered, this was classified by the Nature Conservancy Council as a notable 'B' species (found in less than 100, 10 kilometre squares) Boyce pers. com. (1991). However, with only five specimens recorded over the 14 months field study, little can be deduced from the results. Much of the interest in the conservation of woodland invertebrates has emphasised the invertebrates associated with the early and late successional stages of woodland vegetation

Harding and Rose (1986), Key and Warren (1991). Despite this Chalmers-Hunt (1969), Warren and Fuller (1990), have drawn attention to the importance of varied structure and the need for a full representative range of habitat mosaics within individual sites, to maintain invertebrate assemblages of high diversity. Hammond (1974), agreed and notes in the South-East of England that "Although the number of *coleopterous* species have remained relatively constant throughout the historical period, the rise to dominance of synanthropic species and the spread of new immigrants is leading to increased uniformity". Nearly all of the *carabid* species recorded at High Beach, Epping Forest, have been identified as eurytopic species, Luff (1982), *carabids* that are common and ubiquitous which in themselves are of little conservation value. However, as Bratton (1991), has suggested invertebrates are often sensitive indicators of environmental change and it is from this perspective that the true worth of the *carabid* assemblages at High Beach, Epping Forest can be appreciated. The changes in physical and chemical environmental factors, induced by extensive management of the woodland ecosystem are picked up by the dynamic fluctuations in the distribution of *carabid* assemblages. Rushton, Luff and Eyre (1991), recognised the value of predicting the abundance of species from environmental gradients and the present study attempted this. The results showed that the most abundant *carabid* species: *Notiophilus biguttatus*, *Nebria brevicollis* and *Calathus piceus*, at High Beach showed a preference for high humidity, produced by the leaf litter depth, which itself varies as a result of the stage of ecological succession of the woodland vegetation. Further, ground light intensity increases after pollarding Rackham (1978), and as there is a direct relationship between the abundance of *Loricera pillicornis* and ground temperature, (which itself is mostly dependent on solar radiation) in the present study it seems likely that pollarding would affect the distribution of this species. Considering these two points the results of the present study show that the greater number of *carabid* species are found in the *Fagus* stands (27) in contrast with *Betula* stands (17). Equally the Mean number of *carabids* per pitfall, per day is greater in the *Fagus* (72.7) stands compared to *Betula* (42.3) stands. Because of the neglect of the *Fagus* pollards the general leaf litter depth has probably increased during the last 100 years, as the pioneer *Betula* colonised the sites where pollarded *Fagus* crowns have toppled. Measurements of the mean light

intensity show that the *Fagus* sites with their vast overgrown crowns in fact have a greater light intensity (51.2%) than the *Betula* stands (35.2%), i.e. *Fagus* sites are brighter than *Betula* sites.

Both these points suggest that a return to active pollarding would not only increase light intensity but also reduce the general leaf litter depth. Figure 17 illustrates drawings originally presented by Buxton (1885), these depict two sites in Epping Forest, one of which had been recently pollarded, whilst the other had not.

Figure 17. Drawings originally presented by Buxton (1885), depicting two sites in Epping Forest, one of which was recently pollarded whilst the other has been neglected for 10 to 15 years. The pollards at High Beach have probably been neglected for over 100 years.



Fry and Lonsdale (1991), have pointed out that the invertebrates that inhabit leaf litter essentially promote the breakdown of recently fallen leaves into humus. The depth of leaf litter is greater in the *Betula* sites (mean 5.7cm) than at the *Fagus* sites (mean 2.3cm) and the mean number of invertebrates is greater in the *Betula* sites (10.5) than the *Fagus* sites (6.1). This suggests that the majority of the invertebrates at High Beach, Epping Forest are those which fulfil the role of leaf litter breakdown, or prey on those which do. Whereas in the past, when pollarding was carried out rigorously, the ground fauna would have consisted of invertebrates adapted to open ground.

If conservation interests suggest a shift from an invertebrate fauna which is primarily concerned with leaf litter decomposition to one that is dependent on open ground with high light intensities, a return to pollarding would appear essential. However, as has been pointed out earlier, the conservation value of any site is enhanced by a mosaic of different habitats and so wholesale pollarding on a large scale should be avoided. Instead this should take place over a period of decades to encourage a successional spectrum of different vegetation age types, which itself would generate a wide variation in the environmental gradients present at the site. The removal of many of the young *Betula* stands and the positive encouragement of *Fagus* regeneration by planting or with the use of exclosures (to avoid the attention of the large rabbit population at High Beach) would help deflect the present succession which is heading towards *Betula* domination and help increase the age range of the *Fagus* population at the site. It is possible that the physical removal of leaf litter (as gravel and turf were removed by traditional management practices) may also be necessary to reduce the nutrient status of the site. A policy to encourage the spread of the traditional grassy plains, would also enhance the invertebrate diversity, encouraging the flora and fauna associated with that of past management regimes. In general terms these recommendations are in line with those put forward by Webster (1991).



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## Appendix 1.

This list collates all carabid species discovered in the literature as recorded at Epping Forest during the research stage of the present work.

Species indicated to occur at High Beach are denoted by  $\Omega$ . Those that are widely distributed in Epping Forest are indicated by † and those species also recorded in the present study are signified thus ¥.

List according to Buck, (1955).

*Cicindela campestris*  $\Omega$ , *Calasoma inquisitor* †, *C. sycophanta*, *Carabus arvensis*  $\Omega$ , *C. granulatus*, *C. nemoralis* †, *C. problematicus* †, *C. violaceus* ¥, *Cychrus caraboides*  $\Omega$ ¥, *Leistus spinibarbis*, *L. fulvibarbis*  $\Omega$ , *L. ferrugineus* ¥, *Nebria brevicollis* ¥†, *Notiophilus aquaticus*, *N. palustris*  $\Omega$ , *N. substriatus*, *N. rufipes*  $\Omega$ ¥, *N. biguttatus* †¥, *Elaphrus riparius*, *Loricera pilicornis*  $\Omega$ ¥, *Clivina fossor*, *Dyschirius ludersi*, *Asaphidion flavipes*  $\Omega$ ¥, *Bembidion lampros*†¥, *B. dentellum*  $\Omega$ , *B. nitidulum*  $\Omega$ ¥, *B. rupestre*  $\Omega$ , *B. ustulatum*, *B. genei*  $\Omega$ , *B. gilvipes*, *B. assimile*  $\Omega$ , *B. transparens*  $\Omega$ , *B. minimum*, *B. quadrimaculatum*, *B. doris*  $\Omega$ , *B. articulatum*  $\Omega$ , *B. obtusum*, *B. harpaloides*  $\Omega$ ¥, *B. biguttatum*, *B. aeneum* †, *B. unicolor*, *B. guttula* ¥, *B. lunulatum*, *Trechus secalis*, *T. quadristriatus*, *Harpalus latus*  $\Omega$ , *H. tardus*  $\Omega$ , *H. angusticollis*, *Stenolophus mixtus* †, *Acupalpus dorsalis*, *A. luridus* †, *A. exiguus*  $\Omega$ , *A. consputus*, *Bradycellus ruficollis*, *B. verbasci*, *B. harpalinus* †, *Amara plebeja*  $\Omega$ , *A. ovata*, *A. montivaga*, *A. convexior*, *A. vulgaris* †, *A. aenea*  $\Omega$ , *A. familiaris* †, *A. tibialis*, *A. aulica*, *Stomis pumicatus*, *Pterostichus cupreus*, *P. macer*  $\Omega$ , *P. niger* †¥, *P. minor*  $\Omega$ , *P. nigrita* †¥, *P. strenuus* ¥, *P. diligens* †, *P. madidus*  $\Omega$ ¥, *Abax parallelepipedus* † $\Omega$ , *Platyderus ruficollis*  $\Omega$ , *Calathus fuscipes* ¥, *C. melanocephalus* ¥, *C. piceus* ¥, *Odontonyx rotundatus*, *Agonum sexpunctatum*, *A. marginatum*, *A. versutum*  $\Omega$ , *A. viduum*, *A. assimile*  $\Omega$ ¥, *A. ruficorne*, *A. obscurum* †¥, *A. dorsale*, *A. micans*  $\Omega$ , *A. fuliginosum* †, *A. piceum*, *A. gracile* †, *A. thoreyi*, *Demetrius atricapillus* †, *Dromius linearis* †, *D. agilis*  $\Omega$ , *D. meridionalis*  $\Omega$ , *D. quadrimaculatus* †, *D. quadrinotatus* †¥, *D. sigma*, *D. melanocephalus* †, *Metabletus obscuroguttatus*, *M. foveatus*, *Microles maurus*, *Polistichus connexus*, *Brachinus crepitans*.

Hammond's additions, (1979).

*Leistus rufescens*, *Nebria salina* ¥, *Elaphrus cupreus*, *Patrobus atrorufus*, *Bembidion varium*, *Pterostichus angustatus* ¥, *P. longicollis*, *P. melanarius*, *P. vernalis*, *P. versicolor*, *Synuchus nivalis*, *Laemostenus terricola*, *Agonum*



*muelleri*, *Amara similata*, *Harpalus rufipes*, *Bradycellus sharpi*, *Badister sodalis*, *Chalaenius vestitus*, *Demetrias imperialis*.

Possible\* additions from the Essex Biological Records Centre, (Pers. comm. Plant, 1991).

*Bembidion mannerheimi*, *Amara bifrons*, *Sphodrus leucophthalmus*.

Additions from the N.N.C. Invertebrate Site Register, (Pers. comm. Dagley, 1991b).

*Bembidion quadripustulatum*, *Amara anthobia*, *Harpalus attenuabus*.

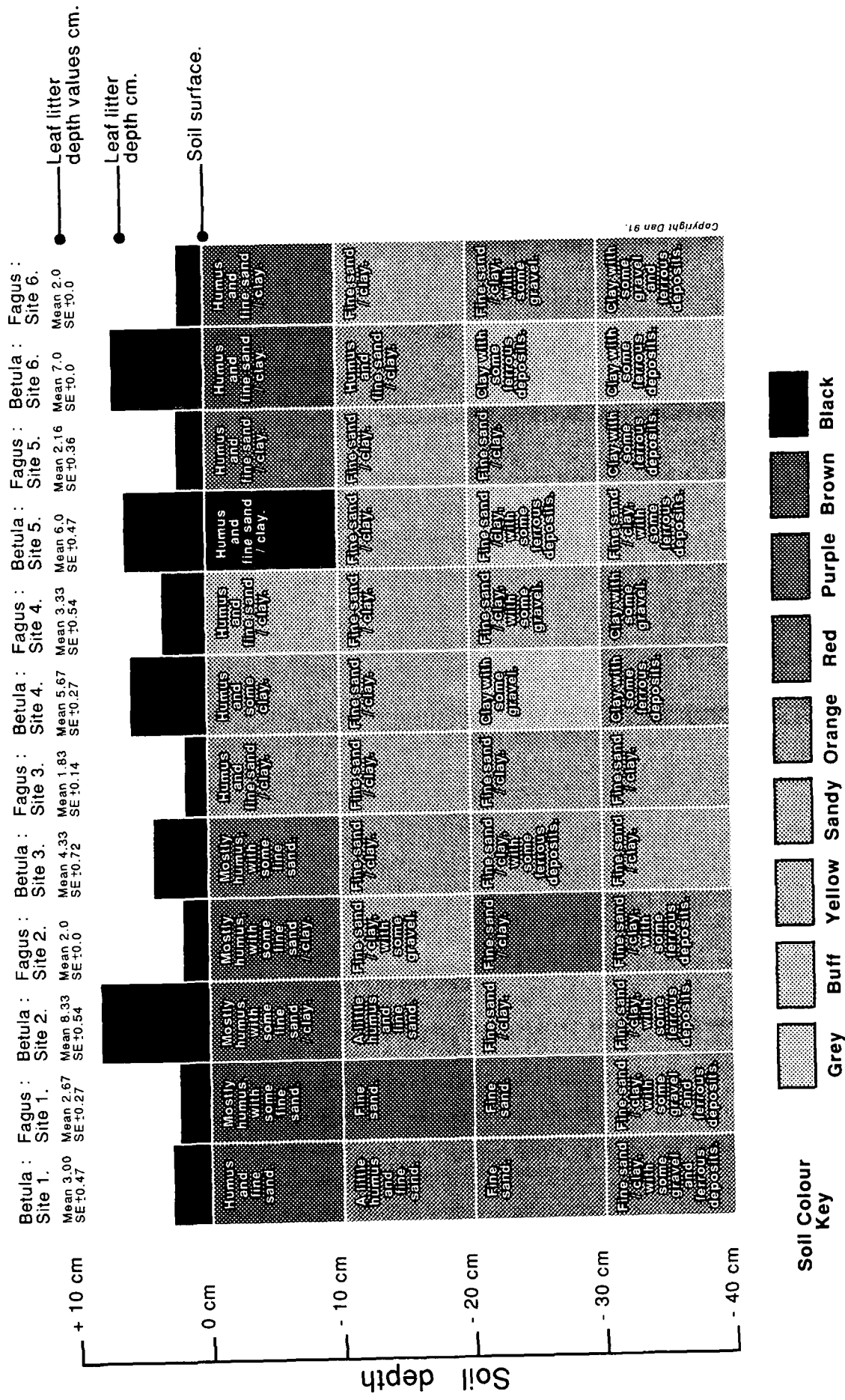
New species recorded by the present study.

*Leistus rufomarginatus*, *Trechus obtusus*, *Bembidion tetracolum*.

\* These records were determined by relating a grid reference on a computer printout to a relevant O.S. map. Since in some cases the grid reference was less than a six figure reference, absolute certainty that these results occur within the official Epping Forest boundary can not be guaranteed.

## Appendix 2. Generalised soil profiles of study sites, High Beach, Epping Forest.

At each study site, using a half metre auger, three soil profiles were recorded. The results have been summarised in the table below. The colours of the soil, have been transcribed as tones of grey. Although this is not a perfect way of illustrating the differences, until colour printing technology becomes freely available, such efforts will have to suffice. The black columns above the soil surface represent the mean leaf litter depth, at each site.



Copyright Dan 91.

Total Data		Appendix 3. Mean number of carabids, per pitfall, per day, recorded from High Beach, Epping Forest.																														
Sites	Stand	Abax parallelipipedus	Agonum assimile	A. obscurum	Asaphidion flavipes	Bembidion guttula	B. harpaloides	B. lampros	B. nitidulum	B. tetracolum	Calathus fuscipes	C. melanocephalus	C. piceus	Carabus violaceus	Cychrus caraboides	Dromius quadrinotatus	Leistus ferrugineus	L. rufomarginatus	Loricera pilicornis	Nebria brevicollis	N. salina	Notiophilus biguttatus	N. rufipes	Pterostichus angustatus	P. diligens	P. madidus	P. niger	P. nigrita	P. strenuus	Trechus obtusus	Total	
1	Fagus	0.1	-	-	0.1	0.3	0.9	-	-	-	0.1	2.4	4.6	-	0.1	-	-	0.1	-	1.4	0.2	1.2	-	-	-	-	0.2	-	-	-	11.8	
	Betula	0.9	0.1	-	-	-	-	-	-	-	-	0.4	3.0	-	-	-	-	-	-	5.6	1.4	0.7	0.8	-	-	-	-	-	-	-	12.9	
2	Fagus	0.7	-	-	-	-	-	-	-	-	-	1.2	1.2	-	-	0.2	0.1	-	-	4.0	0.7	1.1	1.2	-	-	-	-	-	-	-	10.2	
	Betula	2.5	-	-	0.2	-	-	-	-	-	-	0.1	0.1	-	-	-	0.1	-	-	0.2	-	0.3	-	-	-	0.3	-	-	-	-	-	3.7
3	Fagus	0.5	0.5	0.1	1.8	0.1	-	2.5	0.3	0.1	-	-	0.5	0.2	-	-	-	-	-	1.6	1.3	-	0.8	-	0.1	-	0.1	-	0.2	-	-	10.5
	Betula	5.7	0.3	-	-	-	-	-	-	-	-	-	1.4	0.4	-	-	-	-	0.4	-	1.2	0.1	0.2	0.1	-	-	0.3	-	-	-	-	9.9
4	Fagus	0.2	-	-	-	-	-	-	-	-	-	-	3.9	0.1	-	-	-	-	-	0.3	3.6	-	0.6	0.1	-	-	-	-	-	0.2	8.9	
	Betula	1.3	-	-	-	-	-	-	-	-	-	-	0.8	2.4	-	-	0.5	0.1	0.3	0.2	-	0.5	0.2	-	-	0.1	-	0.5	-	-	6.9	
5	Fagus	-	-	-	0.5	-	-	0.5	-	-	-	0.8	7.3	-	-	-	-	-	-	0.5	5.8	0.2	2.7	0.5	0.4	-	0.8	-	0.1	-	0.4	20.4
	Betula	2.0	-	-	-	-	-	-	-	-	-	-	0.6	1.3	-	-	-	-	-	0.3	1.3	0.2	0.1	-	-	0.1	-	-	0.3	-	6.1	
6	Fagus	0.3	-	-	0.1	-	-	0.2	-	-	-	-	4.4	-	-	-	-	-	-	0.1	2.5	0.4	2.5	-	0.2	-	0.1	-	-	-	-	10.9
	Betula	1.0	-	-	-	-	-	-	-	-	-	-	0.2	1.0	-	-	-	-	0.1	-	0.2	-	0.3	0.1	-	-	-	-	-	-	2.8	
Total	Fagus	1.8	0.5	0.1	2.5	0.4	0.9	3.2	0.3	0.1	0.1	4.4	22.0	0.3	0.1	0.2	0.1	0.1	2.5	18.6	1.6	8.8	1.7	0.7	-	1.0	0.2	0.3	-	0.5	72.7	
	Betula	13.4	0.4	-	0.2	-	-	-	-	-	-	0.5	6.1	5.1	-	-	0.6	0.6	0.6	8.5	1.7	2.1	1.1	-	0.1	0.7	-	0.5	0.3	-	42.3	



**Appendix 5. Mean environmental data**

<b>Variables</b>	<b>Sites</b>	<b>Fagus site 1</b>	<b>Fagus site 2</b>	<b>Fagus site 3</b>	<b>Fagus site 4</b>	<b>Fagus site 5</b>	<b>Fagus site 6</b>	<b>Betula site 1</b>	<b>Betula site 2</b>	<b>Betula site 3</b>	<b>Betula site 4</b>	<b>Betula site 5</b>	<b>Betula site 6</b>
Gradient (degrees)		9	4	8	5.5	1.5	4.5	3	7	10	5	4	9
Number of Fagus leaves per 250ml		22.0	6.0	17.7	12.0	13.3	21.0	40.3	56.7	22.7	12.7	24.3	53.0
Light (%) intensity		37.3	49.0	38.8	72.0	66.0	44.2	27.5	24.8	22.8	62.0	54.5	18.7
Soil depth (cm) (Humus layer)		7.5	6.8	7.8	5.83	3.5	3.8	11.2	17.5	11.7	9.8	12.0	11.0
Soil pH		4.1	3.8	4.3	4.0	4.1	4.0	3.9	3.4	4.2	4.0	3.8	3.7
Soil water content (%)		41.0	51.9	49.3	40.2	47.2	45.4	38.6	59.2	51.5	59.7	48.5	49.9
Soil organic content (%)		7.7	28.6	18.0	19.4	19.6	18.7	15.3	29.1	27.3	18.1	22.3	25.9
Vegetation cover (%)		1.3	9.2	17.3	0	2.5	1.7	0.6	0	0	36.0	35.0	32.8
Leaf depth (cm)		2.7	2.0	1.8	3.3	2.2	2.0	3.0	8.3	4.3	5.7	6.0	7.0
Leaf water content (%)		21.4	25.6	40.7	51.0	32.4	43.6	36.1	68.6	61.7	67.6	63.71	65.5
Temperature at ground level (C°)		17.9	18.5	22.0	19.3	19.1	19.3	19.4	17.2	18.7	18.0	20.0	19.0
Distance to the nearest tree (cm)		267.5	349.0	321.2	485.2	293.0	454.8	95.7	98.5	91.8	150.0	132.5	123.2
Circumference of nearest tree (cm)		185.3	196.2	194.0	324.3	173.0	104.8	25.5	13.7	27.0	46.7	13.8	21.5

Appendix 6. The mean percentage cover of vegetation per 0.25 m <sup>2</sup> quadrat																
Sites :																
Cover agents :	F 1	F 2	F 3	F 4	F 5	F 6	B 1	B 2	B 3	B 4	B 5	B 6	Total Mean Fagus	Total Mean Betula		
1. Algae spp. (unidentified)	-	5.8	-	-	-	1.7	-	-	-	-	-	-	1.3	-		
2. Leucobryum glaucum	1.3	-	1.3	-	1.5	-	-	-	-	-	-	-	0.7	-		
3. Pteridium aquilinum	-	-	-	-	-	-	-	-	-	21.7	-	-	-	3.6		
4. Lonicera periclymenum	-	-	-	-	-	-	-	-	-	7.7	-	-	-	1.3		
5. Rubus fruticosus	-	-	-	-	-	-	-	-	-	6.7	34.2	32.5	-	12.3		
6. Dactylis glomerata	-	-	0.1	-	-	-	-	-	-	-	-	-	0.1	-		
7. Deschampsia flexuosa	-	3.3	0.4	-	0.8	-	-	-	-	-	-	-	0.8	-		
8. Poa annua	-	-	0.1	-	0.2	-	-	-	-	-	-	-	0.5	-		
9. Juncus bufonius	-	-	13.8	-	-	-	-	-	-	-	-	-	2.3	-		
10. Betula spp. seedlings	-	-	1.7	-	-	-	0.6	-	-	-	-	-	0.3	-		
11. Betula spp. trees	-	-	-	-	-	-	-	-	-	-	0.8	-	-	0.1		
12. Roots	3.3	1.7	3.3	0.4	1.7	0.8	-	-	-	-	-	-	1.9	38.4		
13. Old leaf litter	57.9	50.0	36.3	42.9	9.2	59.2	42.3	50.0	50.0	21.9	32.5	33.8	42.6	40.9		
14. New leaf litter	37.5	32.1	18.3	56.7	9.2	35.8	57.1	50.0	50.0	21.9	32.5	33.8	31.6	3.2		
15. Bare soil	-	7.1	25.0	-	77.5	2.5	-	-	-	19.4	-	-	18.7	-		

